# The vegetation ecology and native status of Scots pine (*Pinus sylvestris* L.) in Ireland

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## Declaration

I hereby declare that this thesis has not been submitted as an exercise for a degree at this or any other university and that it is entirely my own work. I agree that the library may lend or copy this thesis upon request.

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## Summary

This thesis examines the vegetation ecology, native status and biodiversity value of Scots pine (*Pinus sylvestris* L.) in Ireland, using a variety of biogeographical, palaeoecological and ecological approaches at different spatial and temporal scales. *P. sylvestris* is known to have colonised Ireland relatively early in the postglacial, becoming an important component of certain marginal habitats before undergoing a dramatic decline. The species is widely believed to have been extirpated during the early medieval period. *P. sylvestris* had been reintroduced to Ireland by the eighteenth century and is currently widespread and naturalising in semi-natural habitats. Ireland's Native Woodland Scheme provides financial incentives for the planting of native trees of local provenance. Despite its uncertain native status, *P. sylvestris* has been included in this scheme and is being widely planted in semi-natural habitats. Few studies have addressed the autecology and vegetation ecology of the species in the Irish context. Information on its native status, ecological requirements and biodiversity value is urgently required to inform conservation and forest management strategies.

A database of site attributes and *Pinus* pollen frequencies from 84 palynological sampling sites throughout Ireland was compiled and added to a Geographic Information System. Isopoll maps were prepared at 500 year intervals in order to illustrate the dynamics of *Pinus* in Ireland throughout the Holocene. Spearman's rank correlation coefficients for mean *Pinus* pollen frequencies and site attributes were calculated for each time interval. The arrival, expansion, decline and reintroduction of *Pinus* were clearly illustrated by the isopoll maps. *Pinus* pollen frequencies were significantly correlated with altitude and location during various periods of the Holocene. These results generally supported previously described patterns. However, the isopoll maps suggested that high *Pinus* pollen frequencies persisted in localised areas of western Ireland during the period when *Pinus* was thought to be extinct in Ireland.

The vegetation history of an apparently naturalised pinewood in the Burren over the last 2000 years was examined, with particular reference to the *Pinus* decline. A relatively stable vegetation history was recorded, despite considerable human activity. The dominant vegetation type was an open pinewood with abundant *Corylus*. Remarkably, no *Pinus* decline was recorded. *Pinus* pollen frequencies consistently exceeded 38% and macrofossil evidence demonstrated the local presence of *Pinus* at about AD 840. This indicated that a relict population of *P. sylvestris* has persisted in the Burren to the present day, challenging the established view that *P. sylvestris* became extinct in Ireland.

Botanical surveys were conducted in 20 *P. sylvestris* woodland plots in Ireland and seven in Scotland. Vegetation, structural and environmental data were analysed using non-parametric and multivariate statistical techniques and synoptic tables were prepared. In the Irish context, *P. sylvestris* was found to tolerate a wide range of environmental conditions. Soil pH, altitude and slope had important roles in partitioning four reasonably well defined vegetation communities, some of which corresponded to habitats of international conservation importance. Irish pinewoods were found to form an important resource for the conservation of native botanical and habitat diversity. The Irish plots were compared quantitatively with native pinewoods of high biological quality in Scotland and qualitatively with native pinewood types in continental Europe. Each Irish pinewood type was found to correspond, to a greater or lesser extent, to its native counterparts. Irish pinewoods were found to function as native ecosystems.

*P. sylvestris* woodlands are a common feature in the Irish landscape, although they are fragmented and limited in extent compared to their former range. For practical conservation purposes, *P. sylvestris* should be managed as a native species in woodland habitats in Ireland. *P. sylvestris* offers forestry potential, native status, broad ecological tolerances and has the potential to support native biodiversity. It therefore has the potential to make a significant, positive contribution to biodiversity conservation and sustainable forest management in Ireland.

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# 1. General Introduction

Much of Europe's original forest was cleared in prehistoric times. The remaining natural forests have either been modified by centuries, and sometimes millennia, of management or are secondary formations on land which was previously cleared. Few, if any, examples of virgin forest remain, particularly in north-west Europe. However, attitudes to forest conservation have changed greatly, particularly in recent decades (Peterken, 1996). Although deforestation is a major driver in the loss of biodiversity (Wilson & Peter, 1988) and remains a significant global concern, most European countries are now showing a net increase in forest area (FAO, 2007). Efforts have been made to conserve existing natural forests, re-establish native forests and to manage plantations in a manner that is more sympathetic to the conservation of biodiversity (Peterken, 1996; Hartley, 2002).

Restoration (the augmentation or re-establishment of an extinct population or community) is a valuable tool in mitigating habitat loss (McKay *et al.*, 2005). The restoration of natural forests has been a common management objective since the establishment of the earliest forest reserves in the nineteenth century (Peterken, 1996). The classification of species as either native or non-native is one of the organising principles of restoration ecology, and conservation biology in general. However, the concept, language and practice of this classification have been subject to substantial criticism. For example, our limited and fragmentary knowledge of human history and of the biogeography and palaeoecology of individual species mean that it may be difficult to unambiguously determine the past distribution and native status of a given species (Webb, 1985; Warren, 2007). Although it has been proposed that conservation managers should focus on the behavioural traits and ecological characteristics of species (i.e. their potential to disrupt ecosystem services) rather than their origins (Smout, 2003; Warren, 2007), many conservation and forest management strategies remain focused on native

status. For example, it is an important consideration in species selection for sustainable commercial forestry (Higman *et al.*, 2005).

Reintroduction (an attempt to establish a species in an area that was once part of its historical range, but from which it has been extirpated or become extinct) is a key component of restoration ecology (IUCN, 1995). Some examples include the reintroduction of the golden eagle (*Aquila chrysaetos*) to Ireland (O'Toole *et al.*, 2002) and the capercailie (*Tetrao urogallus*) to Scotland's pinewoods (Lever, 1977). Plant reintroductions can play an important role in reinstating the original biological diversity of a degraded area as part of a restoration programme (Maunder, 1992). However, reintroduction also results in the introduction of potentially maladapted non-local, or non-native, genetic material into semi-natural ecosystems (McKay *et al.*, 2005) and therefore presents a dilemma for the conservationist. The native/non-native paradigm, which underlies many conservation strategies, is blurred in the case of reintroduced species.

## 1.1 Study System: *Pinus sylvestris* in Ireland

This thesis aims to explore some of the issues surrounding the native status of Scots pine (*Pinus sylvestris* L.) in Ireland. This study system incorporates the themes of restoration and reintroduction, as discussed above, in the context of the ecology and management of semi-natural and plantation forests in north-west Europe.

### 1.1.1 Study Site

In regions where the area of plantations is high relative to that of natural forests, plantations of non-native species can assume importance as a resource for biodiversity (Brockerhoff *et al.*, 2008). North-west Europe is one such area. In Belgium, Denmark and the UK, for example, plantations constitute 41.0, 63.0 and

67.6% of forest cover respectively. In Ireland, a very low proportion (9.7%) of the land area is forested and a very high proportion of this (86.5%) consists of plantations (FAO, 2007).

Ireland's island status, small size and low coverage of native woodland make it a useful model study side for investigating the contribution that non-native, and questionably native, tree species can make to the conservation of native biodiversity. Due to its glacial history, location at the edge of Europe and, again, its small size and island status, Ireland's native botanical diversity is significantly lower than elsewhere in north-west Europe, with a vascular flora of just 815 species, excluding Pteridophytes and apomictic microspecies (Webb, 1983). Substantial research has been conducted on the vegetation ecology of both native forests (Kelly, 1981; Kelly & Kirby, 1982; Cross, 1987; Cross, 1992; Kelly & Iremonger, 1997; Perrin *et al.*, 2008b) and non-native plantations (Iremonger *et al.*, 2006; French *et al.*, 2008) in Ireland but the ecology of *P. sylvestris*, a reintroduced species, has been largely overlooked.

### 1.1.2 Study Species

Scots pine (*Pinus sylvestris* L.) is a coniferous tree species of the family Pinaceae. Its morphology is described by Carlisle & Brown (1968). It is the most widely distributed pine species in the world (Vidakovic, 1991) and is one of the most commercially important Eurasian forest trees. The native range of *P. sylvestris* covers approximately 14,000 km east to west, from the Pacific coast of north-east Asia to Scotland and the north-west of the Iberian Peninsula, and 2700 km north to south, from northern Norway to southern Spain. The species is widely but discontinuously distributed within these limits (Steven & Carlisle, 1959; Mirov, 1967; Volosyanchuk, 2002). The current natural distribution of *P. sylvestris* in Europe is illustrated in Figure 1.1.

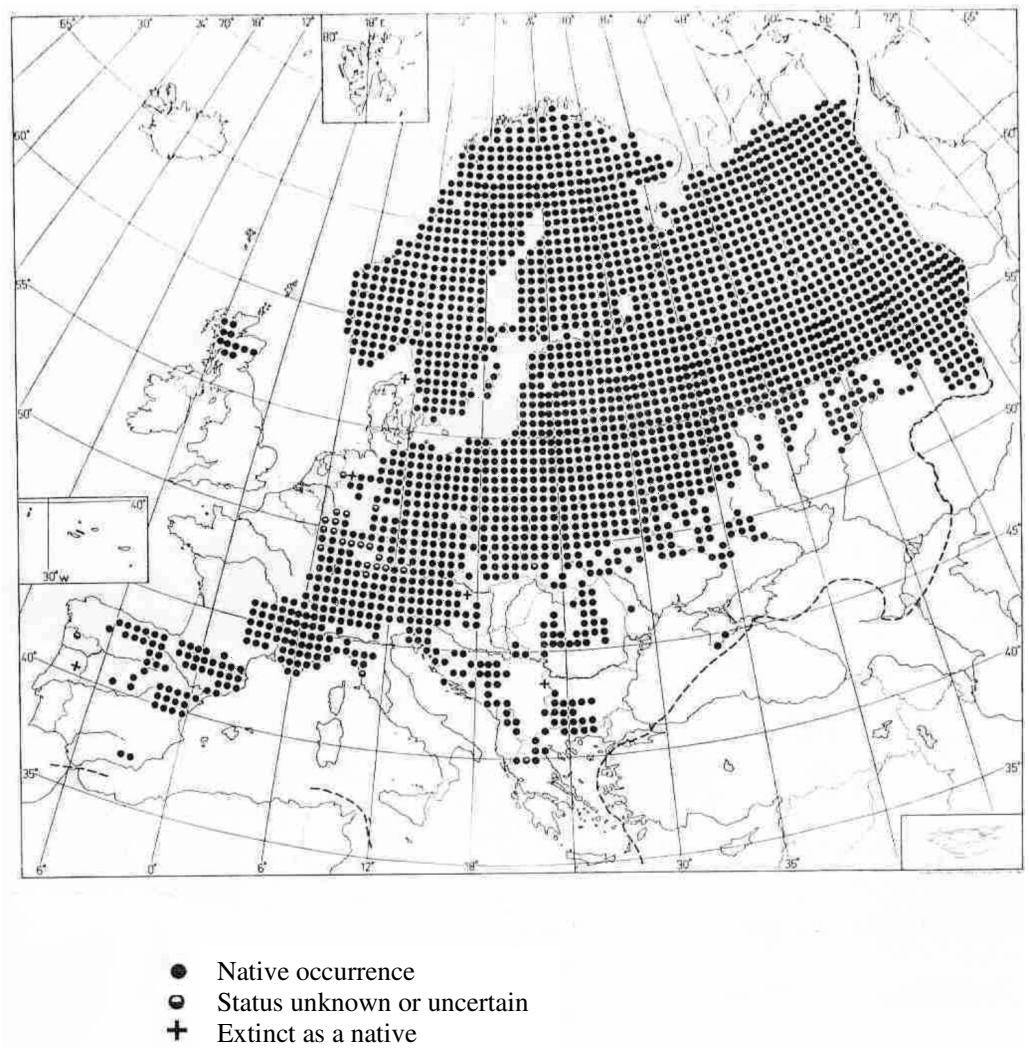



Figure 1.1. Current natural distribution of *Pinus sylvestris* in Europe (Jalas & Suominen, 1973).

This wide geographic range reflects the extraordinarily broad ecological amplitude of *P. sylvestris*, as evidenced by the diversity of climatic conditions it tolerates, from severe cold in northern Siberia to the Mediterranean climate of southern Spain and from the wet, oceanic climate of western Scotland to the dry continental climate of central Europe and Asia (Carlisle & Brown, 1968). In Europe, pines generally occupy marginal habitats (Willis *et al.*, 1998). *P. sylvestris* can be found on a wide variety of soil types including podzols, brown calcareous earths with

mull humus, humic rendzinas and deep peats (Aune, 1977; Ellenberg, 1982; Bjørndalen, 1985; Rodwell & Cooper, 1995). *P. sylvestris* may act as a pioneer species, particularly on raised bogs that have suffered drainage or disturbance (Stoll *et al.*, 1994), and forms stable vegetation communities on nutrient-deficient soils, indicating a high competitive ability under these conditions. However, it is light-demanding and will not tolerate heavy shade from other trees (Carlisle & Brown, 1968).

## 1.2 Background and Justification for the Research

The postglacial dynamics of *Pinus* in Europe are described by Huntley & Birks (1983). *P. sylvestris* is the only member of the Pinaceae which is native to the British Isles today and the only species of *Pinus* to have been identified from fossil remains in the British and Irish Pleistocene (Godwin, 1975; West, 1980). It is therefore reasonable to assume that all postglacial plant remains from the British Isles that are identifiable as Pinaceae refer to this species. The postglacial dynamics of *P. sylvestris* in the British Isles are described by Bennett (1984) and in Ireland by Bradshaw & Browne (1987). Briefly, palaeoecological evidence indicates that *P. sylvestris* colonised Ireland by 9500 BP (radiocarbon years before present) (Mitchell, 2006), becoming an important component of marginal habitats such as raised bogs, river valleys and uplands, until a major decline began about 4000 BP (Bradshaw & Browne, 1987). The species is believed to have been extirpated from Ireland around 1600 BP (McAulay & Watts, 1961) but had been reintroduced by the eighteenth century (Pococke, 1891). A more detailed description is provided in Chapter 2.

Inconsistencies exist, however, between the palaeoecological evidence and documentary sources. The literary and linguistic evidence from the Irish language suggests that *P. sylvestris* persisted until at least AD 900 (Kelly, 1976). In addition, recent research questions the methods that palynologists have used to

determine the local presence of *P. sylvestris.* A "critical pollen percentage" of 20% of total pollen (Bennett, 1984) was widely adopted in the interpretation of pollen diagrams as a criterion for the local presence of *P. sylvestris* and has been applied in the Irish context (Bradshaw & Browne, 1987). However, subsequent research has used fossil stomatal guard cells to show the unambiguous local presence of *P. sylvestris* within a sequence despite pollen frequencies being considerably below the 20% threshold (Fossitt, 1994; Cooney, 1996; Froyd, 2005). This provokes the question: did *P. sylvestris* become completely extinct in Ireland or did relict populations or individuals survive beyond 1600 BP, perhaps to the present day? As Watts (1984a) put it,

> "*Why a very widespread species living in many kinds of habitat from Algeria to north of the Arctic Circle should have failed to survive in Ireland is mysterious, especially as pine survives in western Scotland in habitats similar to those from which it had disappeared in Ireland. It is also difficult to imagine any form of burning or exploitation which would cause complete extinction. Further, planted pines thrive today in Ireland and invade natural habitats readily. … The problem is a challenging and interesting one deserving further study*."

A fresh examination of the postglacial dynamics of *P. sylvestris* in Ireland, incorporating new techniques, recent increases in the number and geographical spread of available, dated pollen sequences and additional, targeted palaeoecological analyses, is necessary and would be informative in the investigation of the species' native status.

The modern as well as the historic dynamics of *P. sylvestris* in Ireland are of research interest. Since its reintroduction, *P. sylvestris* has been widely planted in Ireland (Cross, 1998) and is naturalising in a variety of semi-natural habitats (Kelly, 1981, 1985). Earlier in the twentieth century, extensive plantations of it were established but after 1945, more productive exotic species, especially *Picea*

*sitchensis*, became favoured for commercial forestry (O'Driscoll, 1980). *P. sylvestris* is Ireland's only native or "semi-native" conifer species with forestry potential (Forest Service, 2000). Under the strategic plan for the development of the Irish forestry sector, the amount of forested land in Ireland is set to increase substantially from 9.7 to 17.0% by 2030 (Department of Agriculture, 1996; FAO, 2007). Ireland's Native Woodland Scheme provides grant aid to landowners for the planting of native tree species of local genetic provenance. This scheme consists of two elements, the establishment of new native woodlands and the conservation and restoration of existing native woodlands (Forest Service, 2001). Despite its uncertain native status, *P. sylvestris* has been included in this scheme and is being widely planted in semi-natural habitats. These plans for afforestation and woodland restoration are hindered in part by a lack of knowledge of the ecology of *P. sylvestris* in Ireland.

Despite its widespread distribution and continued planting, very few published studies provide vegetation descriptions or classifications applicable to *P. sylvestris* in Ireland. This inadequate treatment is a product of the species' uncertain native status and diminished popularity in commercial forestry. *P. sylvestris* woodlands were excluded from the Irish National Survey of Native Woodland and its associated classification of vegetation communities (Perrin *et al.*, 2008b) and were not formally recorded in White & Doyle's (1982) overview of phytosociological associations in Ireland. Although Fossitt's (2000) broad scale classification of habitats in Ireland makes some limited, non-specific provisions for pinewoods, that scheme was not intended for detailed study and evaluation. O'Connell (1988) conducted a comparative study of contemporary and subfossil pinewoods on raised bogs but otherwise the information gap regarding the plant communities of Irish pinewoods is profound. Data on the vegetation ecology of *P. sylvestris* stands in Ireland and the implications of the species' reintroduction for biodiversity conservation are urgently required to inform ongoing afforestation and woodland restoration initiatives.

## 1.3 Study Objectives and Approaches

The main aim of this study is to contribute to an improved understanding of the ecology, native status and biodiversity value of *P. sylvestris* in Ireland. The results of my investigations into the biogeography, palaeoecology and vegetation ecology of the species at a range of spatial and temporal scales are presented.

The uncertain native status of *P. sylvestris* in Ireland is a product of the species' postglacial dynamics. The elucidation of the rates and mechanisms of spatial and temporal distribution change is critical to our understanding of a species' ecology, present distribution and likely response to future environmental change. In order to meet the objectives of improved understanding of the ecology and native status of *P. sylvestris* in Ireland, it was necessary to collate and review the available data on the species' postglacial dynamics at an all-island scale. This was achieved by compiling a database of pollen data from 84 sites, which could be interrogated in order to describe, analyse and map the postglacial dynamics of *Pinus* in Ireland (Chapter 2).

Such large-scale, biogeographical mapping exercises record gross changes in the distribution of a species but can conceal fine-scale, local patterns that may provide information on the drivers of distribution change. Detailed palaeoecological work is also required to investigate whether contemporary *P. sylvestris* communities originated from relict populations or individuals (Bradshaw & Browne, 1987). In order to meet the objectives of improved understanding of the ecology and native status of *P. sylvestris* in Ireland, it was necessary to examine its dynamics within a single area and to establish the vegetation history of a contemporary pinewood of unknown origin (Chapter 3).

Studies of the palaeoecology and past distribution patterns of *P. sylvestris* provide limited information on the ecology and biodiversity value of contemporary pinewoods in Ireland. Pinewoods have also been consistently overlooked in surveys of Irish woodland habitats. To investigate the biodiversity and ecosystem functioning of *P. sylvestris* woodland in Ireland, it was necessary to carry out vegetation surveys in planted and naturalised pinewoods throughout the country, classify the vegetation types encountered, compare these with previously described Irish vegetation types of known conservation value and to assess spatial diversity within and among these stands (Chapter 4).

To understand the ecology of a plant species in Ireland, the chosen species must also be studied from the broader European perspective (Webb, 1983). Having classified the vegetation of the surveyed pinewoods in the Irish context, the next step was to place them within the phytosociological framework. As the available data suggested that Irish pinewoods originated from reintroduced stock, the assessment of their conservation value would also benefit from a comparison with native stands of high biological quality. It was therefore necessary to examine native pine forests in the nearest countries where such forests occur under comparable environmental conditions (Chapter 5).

To summarise, the layout and specific objectives of this thesis are as follows:

1. To review, analyse and map new and existing palaeoecological data on the postglacial dynamics of *Pinus* in Ireland (Chapter 2).
2. To investigate the late Holocene vegetation history of a pinewood in the Burren, with particular reference to the *Pinus* decline (Chapter 3).
3. To describe the vegetation ecology of planted and naturalised stands of *P. sylvestris* in Ireland and to assess their conservation value (Chapter 4).
4. To compare the vegetation ecology of reintroduced pine forests in Ireland with their native counterparts elsewhere in north-west Europe (Chapter 5).

# 2. GIS-based isopollen maps and postglacial dynamics of *Pinus sylvestris* in Ireland

To be submitted as: Jenni R. Roche, Steve Waldren & Fraser J.G. Mitchell. GIS-based isopollen maps and postglacial dynamics of *Pinus sylvestris* in Ireland. *Annals of Botany*.

Plate 2.1. Photograph of a preserved *P. sylvestris* stump, dating from about 2500 BC (O'Connell *et al.*, 1988), uncovered by turf cutting at Connemara National Park.

## 2.1 Abstract

This study aimed to provide a visual summary of *Pinus* pollen frequencies in Ireland throughout the Holocene and investigate the spatial and temporal dynamics of *Pinus* using statistical analyses.

Site attributes and *Pinus* pollen frequencies from 84 locations throughout Ireland were extracted from databases and the literature and used to construct a Geographical Information System. Isopoll maps were prepared at 500 year intervals from 11,500-0 cal BP, using the inverse distance weighting method of spatial interpolation. Mean *Pinus* pollen frequencies were calculated for each time interval. Spearman Rank correlations were calculated for location, altitude and *Pinus* pollen frequencies.

The arrival, expansion, decline and reintroduction of *Pinus* were clearly illustrated by the isopoll maps and mean *Pinus* pollen frequencies. *Pinus* pollen frequencies were significantly correlated with altitude and location during various periods of the Holocene.

Spatial interpolation using GIS is an effective and objective method of isopoll mapping. The 5% critical pollen percentage is useful as a rough indication of the presence of *Pinus* around a site. The isopoll maps and correlation analyses generally supported accepted patterns in the postglacial dynamics of *Pinus* in Ireland, such as its retreat into upland areas during the *Alnus* expansion and the east-west progression of the decline. However, the isopoll maps suggest that *Pinus* arrived first in western, rather than south-west Ireland and high pollen frequencies persisted in localised areas of western Ireland during the period when *Pinus* was thought to be extinct in Ireland. These patterns warrant further research. The database of dated, regional postglacial pollen sequences presented may be used in meta-analyses of other taxa. Future palynological research would

benefit from stomatal analysis, which provides a better resolved account of the local dynamics of *Pinus*.

## 2.2 Introduction

The availability of palynological databases has made possible a unique series of scientific studies based on a multi-site perspective at large spatial scales, including studies on vegetation dynamics, human impact, genetics and palaeoclimate (Davis, 2009). The elucidation of the rates and mechanisms of spatial and temporal distribution change is very important in our understanding of a species' ecology, present distribution and likely response to future climatic change. Isopoll maps are one of the most effective methods of displaying and summarising large palynological datasets (Birks *et al.*, 1975). The technique was pioneered by Szafer (1935) and involves the plotting of pollen frequencies within a specific geographical area at a known point in time and the drawing of contours ('isopolls') connecting sites of similar pollen values for the taxon of interest. A series of maps is required to illustrate temporal as well as spatial variation. To date, isopoll and isochrone maps have usually been drawn manually, with the contours being positioned to provide the best fit by eye. Palynological datasets are generally large, their interpretation is complex, the data convey spatial and temporal change and data from different sites must often be compared to interpret patterns over large areas (Flantua *et al.*, 2007). Software specifically designed for spatial analysis, such as Geographic Information Systems (GIS), is therefore an ideal tool for handling palynological data and particularly for compiling isopoll maps. Furthermore, standard statistical packages can be linked with GIS for exploratory analysis, statistical analysis and hypothesis testing of environmental data (Burrough, 2001). However, relatively few published studies have employed GIS spatial interpolation techniques for this purpose. Exceptions include Paez *et al.* (2001) and Siska *et al.* (2001), where modern pollen frequencies were mapped using the kriging method, and Perrin (2003), where *Taxus* pollen frequencies in

Ireland from 6000-4600 BP were modelled using the inverse distance weighting method.

This study illustrates the potential for these approaches by utilising data from the European Pollen Database (EPD) (http://www.europeanpollendatabase.net/), Irish Pollen Database (IPAL) (R. Marchant, unpublished) and other sources to examine the dynamics of *Pinus sylvestris* L. (Scots pine) in Ireland from the early Holocene to the present day. Ireland is a model site for such a study, due to its small size, island status and relatively low botanical diversity (Webb, 1983). *P. sylvestris* was selected as a model taxon as more information is available for this combination of taxon, space and time than perhaps for any other (Bennett, 1984). In addition, the case of *P. sylvestris* in Ireland is intriguing because the species was once indigenous and widespread but is believed to have been extirpated and subsequently reintroduced. This pattern of extirpation and reintroduction is also believed to have occurred in England, Wales, Denmark, Belgium and the Netherlands (Mirov, 1967; Jalas & Suominen, 1973; Bennett, 1984; Bradshaw, 1993; Le Maitre, 1998; Lust *et al.*, 2000). The current natural distribution of *P. sylvestris* in Europe is illustrated in Figure 1.1. The extinction of *Pinus* is of particular interest in Ireland as the date varies considerably between regions and the causal factors differ between sites (Watts, 1984a).

*Pinus* isopoll maps have previously been published at the European scale for each millennium from 1000-13,000 BP (Huntley & Birks, 1983), for the British Isles at 5000 BP (Birks *et al.*, 1975) and for Ireland at 5000 and 5200 BP (Bradshaw, 1993, 2001). Isochrone mapping is a related technique which involves the drawing of contours connecting sites at which pollen stratigraphical events occurred simultaneously. These events typically include the arrival and spread of tree taxa. Isochrone maps of the arrival of *Pinus* have been published for the British Isles (Birks, 1989) and Ireland (Mitchell, 2006).

The criteria that indicate the presence of a taxon within the pollen source area of a site are a source of debate among palynologists. This is particularly true of *P. sylvestris*, due to the complex relationship between its pollen frequency and tree numbers within a given area. *P. sylvestris* pollen is usually abundantly produced, wind-borne and well dispersed, so the species is generally considered to be over-represented in the pollen rain relative to other forest trees (Bradshaw, 1981). Tipping (1989) demonstrated that in an open, late glacial landscape in western Scotland, *Pinus* pollen frequencies arising from long distance transport could reach 40% of total terrestrial pollen. Similarly, exaggerated *Pinus* pollen frequencies are recorded from the late glacial at many Irish sites (Telford, 1977; Craig, 1978; Browne, 1986; Barnosky, 1988; Andrieu *et al.*, 1993; Fossitt, 1994). In modern landscapes, significant amounts of *Pinus* pollen have been found in lake sites where no source trees were recorded within a 30 km radius (Bradshaw & Webb, 1985). A "critical pollen percentage" was therefore widely adopted in the interpretation of pollen diagrams as a criterion for the local presence of *P. sylvestris*. Bennett (1984) proposed a minimum frequency threshold of 20% of total pollen, which became commonly accepted. This criterion was used to determine whether *P. sylvestris* was a significant component of the surrounding vegetation or if it was scarce or absent. It has been applied in the Irish context (Bradshaw & Browne, 1987).

More recent research has used fossil stomatal guard cells to show the unambiguous local presence of *P. sylvestris* within a sequence despite pollen frequencies being considerably below the 20% threshold. Bennett (1995) revised the critical pollen percentage to 5%. However, stomata have been recorded with *Pinus* pollen frequencies of 2.8% in sediments from Donegal, north-west Ireland (Fossitt, 1994), 2.3% in Kerry, south-west Ireland (Cooney, 1996) and 0.4% in the Scottish Highlands (Froyd, 2005). Indeed, *P. sylvestris* pollen productivity is known to be low under certain sub-optimal conditions. Occasional pine trees growing on peat, for example, are thought to have minimal impact on the pollen signal (O'Connell & Molloy, 2001). In Poland, Dąbrowski (1975) found that the R-value (calculated

by dividing the percentage frequency of a taxon in surface pollen samples by its percentage frequency in the regional vegetation) of *Pinus* was 4.42 on mineral soil and 0.61 on raised bog. The abundance of *Pinus* on peatlands may therefore have been underestimated. These findings point to the need for a reassessment of the postglacial history of *P. sylvestris* in Ireland, using revised criteria. Unfortunately, relatively few authors provide data on *Pinus* stomata or macrofossils in the Irish context. Some exceptions include Watts (1984a), Fossitt (1994), Cooney (1996), Jennings (1997), Mighall *et al*. (2004) and Molloy and O'Connell (2004). Consequently this review must be based mainly on palynological data, for which a more comprehensive dataset is available. One advantage of this approach is that the more continuous nature of pollen sequences enables us to determine absence and changes in the abundance of taxa in a way which is not usually possible with macrofossil or stomatal evidence (Bennett, 1984).

It has been over 20 years since the last review of the postglacial history of *P. sylvestris* in Ireland (Bradshaw & Browne, 1987). Froyd (2005) called for a reassessment of analyses of the postglacial dynamics of *P. sylvestris*, because many previous studies relied on excessively high critical pollen percentages. The present review is justified by its incorporation of recent increases in the number and geographical spread of dated Irish pollen sequences and its avoidance of the 20% critical pollen percentage. This paper aims to provide a visual summary of the spatial and temporal dynamics of *P. sylvestris* in Ireland from 11,500 to 0 cal BP, including its arrival, expansion, decline and reintroduction, based on a large dataset of palynological sequences. The interpolated pollen frequencies are interpreted conservatively, with reference to macrofossil and stomatal data where available.

## 2.3 Methods

### 2.3.1 Site Selection

The EPD (http://www.europeanpollendatabase.net/) and IPAL (R. Marchant, unpublished) databases and published and unpublished sources were accessed in order to assemble a database of *Pinus* pollen frequencies covering Ireland during the Holocene. Eighty four pollen sequences were selected on the basis of geographical spread (Fig. 2.1), inclusion of radiocarbon or tephra dating and pollen sampling properties. The selection was restricted to sequences taken from lakes or bogs, as these sites recruit pollen from a relatively large area and would permit the reconstruction of *P. sylvestris* dynamics at a regional scale (Jacobson & Bradshaw, 1981). The distribution of sites was non-uniform, but this was unavoidable due to the absence of dated pollen sequences from certain parts of Ireland.

### 2.3.2 Data Collection

The site type, Irish grid reference, altitude, bedrock geology, number of radiocarbon or tephra dates, pollen count and pollen sum calculation were noted for each sequence. All but two sites had a mean pollen sum of at least 300 terrestrial pollen grains. Most sequences used a pollen sum calculation of total identifiable terrestrial pollen excluding local taxa i.e. obligate aquatics in lake sites and bog taxa in peat profiles. Some sequences used total or arboreal pollen sums but were retained in the dataset to maximise the information available (Table 2.1). Calibrated age-depth curves were constructed, where necessary. There was considerable variation in the dating resolution of the profiles used and it was sometimes necessary to extrapolate above or below a sequence of dates. The percentage frequency of *P. sylvestris* pollen was recorded from each sequence at 500 year intervals, covering the full Holocene from 11,500 to 0 calibrated years BP.

Table 2.1. Location (Irish grid), site type, pollen sum and data sources of pollen sequences used in isopoll mapping and shown in Figure 2.1.

| Site | Name | Type | County | Eastings | Northings | Pollen Sum | Reference |
|---|---|---|---|---|---|---|---|
| 1 | Garry Bog | Raised Bog | Antrim | 294000 | 429000 | TP excl. *Sphagnum* | (Hall, 1998) |
| 2 | Lough Nadourcon | Blanket Bog | Donegal | 205000 | 422000 | TP | (Telford, 1977) |
| 3 | Lough Nabraddan | Lake | Donegal | 177700 | 419500 | TTP & vascular plant spores | (Fossitt, 1994) |
| 4 | Altar Lough | Lake | Donegal | 175200 | 419100 | TTP & vascular plant spores | (Fossitt, 1994) |
| 5 | Fallahogy | Raised Bog | Derry | 293000 | 407000 | AP excl. *Corylus* | (Smith & Willis, 1962) |
| 6 | Ballyscullion East | Raised Bog | Antrim | 298900 | 395500 | TP | (Hall *et al.*, 1993) |
| 7 | Ballyscullion | Raised Bog | Antrim | 299800 | 395300 | TP | (Pilcher *et al.*, 1971) |
| 8 | Sluggan Bog | Raised Bog | Antrim | 309900 | 392100 | TTP excl. peatland taxa | (Smith & Goddard, 1991) |
| 9 | Lough Mullaghlahan | Lake | Donegal | 169900 | 392000 | TTP & vascular plant spores | (Fossitt, 1994) |
| 10 | Slieve Gallion | Upland Blanket Bog | Tyrone | 281800 | 388200 | TP | (Pilcher, 1973) |
| 11 | Beaghmore | Blanket Bog | Tyrone | 268500 | 384300 | TP 0-1000 cal BP<br>AP excl. *Alnus* 1500-8500 cal BP | (Pilcher, 1969) |
| 12 | Lough Catherine | Lake | Tyrone | 236500 | 384000 | - | (Edwards, 1980, 1985) |
| 13 | Ballynagilly | Valley Bog | Tyrone | 274300 | 383700 | TP | (Pilcher & Smith, 1979) |
| 14 | Garvaghullion Bog | Raised Bog | Tyrone | 236500 | 376500 | TP excl. *Sphagnum* | (Hall, 1998) |
| 15 | Killymaddy Lough | Lake | Tyrone | 278300 | 362000 | TTP | (Hirons & Edwards, 1986) |
| 16 | Lough Henney | Lake | Down | 335000 | 358500 | TTP | (Hall, 1989) |
| 17 | Long Lough | Lake | Down | 338000 | 355600 | TTP | (Hall, 1990b) |
| 18 | Slieve Croob | Upland Blanket Bog | Down | 331500 | 345500 | TTP excl. peatland taxa | (Holland, 1975) |
| 19 | Glenulra, Céide Fields | Blanket Bog | Mayo | 105000 | 340000 | TTP excl. peatland taxa | (Molloy & O'Connell, 1995) |
| 20 | Carrivmoragh | Valley Bog | Down | 331000 | 340000 | TTP excl. peatland taxa | (Holland, 1975) |
| 21 | Slieve Naslat | Valley Bog | Down | 333000 | 338000 | TTP excl. peatland taxa | (Holland, 1975) |
| 22 | Cregganmore | Lake | Mayo | 96000 | 337000 | TTP | (McKeever, 1984) |
| 23 | Lackan Bog | Raised Bog | Down | 324000 | 337000 | TTP excl. peatland taxa | (Holland, 1975) |
| 24 | Slish Lake | Lake | Sligo | 175802 | 332859 | TP | (Dodson & Bradshaw, 1987) |
| 25 | Union Wood Lake | Lake | Sligo | 169026 | 329922 | TP | (Dodson & Bradshaw, 1987) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 26 | Butter Mountain | Upland Blanket Bog | Down | 328000 | 328500 | TTP excl. peatland taxa | (Holland, 1975) |
| 27 | Croaghan East | Blanket Bog | Mayo | 105000 | 328000 | TTP excl. peatland taxa | (Dwyer, 1995; Dwyer & Mitchell, 1997) |
| 28 | Garrynagran | Lowland Blanket Bog | Mayo | 110000 | 325000 | TTP excl. peatland taxa | (Jennings, 1997) |
| 29 | Slieve Gullion | Upland Blanket Bog | Armagh | 303100 | 321500 | TP | (Hall, 1990a) |
| 30 | Bunnyconnellan East | Blanket Bog | Mayo | 135000 | 315000 | TTP excl. peatland taxa | (O'Connell, 1990b) |
| 31 | Corslieve Lough | Lake | Mayo | 92700 | 312500 | TTP | (Browne, 1986) |
| 32 | Lough Doo | Lake | Mayo | 128250 | 311750 | TTP | (O'Connell *et al.*, 1987) |
| 33 | Carrowkeel | Blanket Bog | Sligo | 175500 | 311500 | TTP | (Göransson, 1984) |
| 34 | Lough Clevala | Lake | Mayo | 106000 | 311000 | TTP | (Browne, 1986) |
| 35 | Redbog | Raised Bog | Louth | 290000 | 303000 | - | (Weir, 1995) |
| 36 | Lough Anaffrin | Lake | Mayo | 87000 | 301500 | TTP | (Browne, 1986) |
| 37 | Lough Aisling | Lake | Mayo | 95700 | 297700 | TTP | (Browne, 1986) |
| 38 | Lough Avullin, Clare Island | Infilled Lake | Mayo | 70000 | 286000 | TP | (Corcoran, 2001) |
| 39 | Moynagh Lough | Lake | Meath | 282000 | 286000 | - | (Stewart, 1996) |
| 40 | Ballywillin Crannóg, Lough Kinale | Lake | Longford | 238500 | 281500 | - | (Selby *et al.*, 2005) |
| 41 | Brackloon Lough | Lake | Mayo | 97000 | 279000 | - | (von Engelbrechten *et al.*, 2000; Little *et al.*, 2001) |
| 42 | Lough Gowlanagower, Inisbofin | Lake | Galway | 54800 | 266500 | TTP | (O'Connell & Ní Ghráinne, 1994) |
| 43 | Church Lough, Inisbofin | Lake | Galway | 55100 | 265100 | TTP | (O'Connell & Ní Ghráinne, 1994) |
| 44 | Derryinver | Blanket Bog | Galway | 69500 | 261500 | TTP excl. peatland taxa | (Molloy & O'Connell, 1993) |
| 45 | Lough Sheeauns | Lake | Galway | 62500 | 258200 | TTP | (Molloy & O'Connell, 1991) |
| 46 | Connemara National Park | Lowland Blanket Bog | Galway | 71000 | 257000 | AP | (O'Connell *et al.*, 1988) |
| 47 | Lough Maumeen | Lake | Galway | 90700 | 250200 | TTP | (Huang, 2002) |
| 48 | Carbury Bog | Raised Bog | Kildare | 268000 | 236000 | TTP excl. peatland taxa | (van Geel & Middeldorp, 1988) |
| 49 | Cornaher Lough | Lake | Westmeath | 239100 | 234900 | TTP | (Heery, 1998) |
| 50 | Mongan Bog | Raised Bog | Offaly | 202000 | 231000 | TTP excl. peatland taxa | (Parkes & Mitchell, 2000; Barber *et al.*, 2003) |
| 51 | Clara Bog | Raised Bog | Offaly | 225000 | 230000 | TTP excl. peatland taxa | (Connolly, 1999; Crushell *et al.*, 2008) |
| 52 | Glashabaun | Raised Bog | Offaly | 267500 | 229100 | TP | (McNally & Doyle, 1984) |
| 53 | Lough Namackanbeg | *Schwingmoor* Lake | Galway | 113200 | 226900 | AP | (O'Connell *et al.*, 1988) |
| 54 | Derryclure Bog | Raised Bog | Offaly | 235800 | 221000 | TP | (O'Connell, 1990a) |
| 55 | Liffey Head Bog | Upland Blanket Bog | Wicklow | 314200 | 213400 | TTP & spores excl. peatland taxa | (Cole & Mitchell, 2003) |
| 56 | All Saints Bog | Raised Bog | Offaly | 201200 | 211300 | TTP & spores excl. peatland taxa | (Cole & Mitchell, 2003) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 57 | Lios Lairthín Mór | Upland Blanket Bog | Clare | 118000 | 204200 | TTP excl. peatland taxa | (Jeličić & O'Connell, 1992) |
| 58 | Ballyduff Bog | Raised Bog | Tipperary | 200700 | 204200 | TTP excl. peatland taxa | (Stefanini, 2008) |
| 59 | Clonfinane | Raised Bog | Tipperary | 198815 | 203715 | TP | (O'Connell & Doyle, 1990) |
| 60 | An Loch Mór, Inis Oírr | Lake | Galway | 99000 | 202000 | TTP | (Molloy & O'Connell, 2004; Schettler *et al.*, 2006) |
| 61 | Lower Lake, Glendalough | Lake | Wicklow | 311800 | 196600 | TTP | (Haslett *et al.*, 2006; J. Maldonado, unpublished) |
| 62 | Rockforest Lough | Lake | Clare | 135600 | 195300 | TTP | (Roche *et al.*, unpublished, Chapter 3) |
| 63 | Gortlecka | Lake | Clare | 132300 | 195100 | - | (Watts, 1984a) |
| 64 | Arts Lough | Lake | Wicklow | 305800 | 193100 | TP excl. *Isoetes* | (Bradshaw & McGee, 1988) |
| 65 | Kelly's Lough | Lake | Wicklow | 305800 | 190800 | TTP & spores | (Leira *et al.*, 2007) |
| 66 | Molly's Lough | Lake | Clare | 126000 | 188500 | TTP & spores | (Lamb & Thompson, 2005) |
| 67 | Mooghaun Lough | Lake | Clare | 141300 | 171400 | TTP | (Molloy, 2005) |
| 68 | Killoran | Raised Bog | Tipperary | 220000 | 166000 | TTP excl. peatland taxa | (Caseldine *et al.*, 2005) |
| 69 | Derryfadda | Raised Bog | Tipperary | 223000 | 165000 | TTP excl. peatland taxa | (Caseldine *et al.*, 2005) |
| 70 | Borheen Lough | Lake | Tipperary | 189700 | 124500 | TTP | (Leira *et al.*, unpublished) |
| 71 | Coolteen | Infilled Lake | Wexford | 295000 | 123000 | TTP | (Craig, 1978) |
| 72 | Ballinloghig Lake | Lake | Kerry | 43000 | 108000 | TTP & spores | (Barnosky, 1988) |
| 73 | Lough Adoon Hill Bog | Blanket Bog | Kerry | 53000 | 107500 | TTP | (Dodson, 1990b) |
| 74 | Lough Camclaun | Lake | Kerry | 52000 | 107000 | TTP | (Dodson, 1990a) |
| 75 | Belle Lake | Lake | Waterford | 266500 | 105000 | TTP | (Craig, 1978) |
| 76 | Sheheree Bog | Bog/Lake | Kerry | 98500 | 88600 | - | (Mitchell & Cooney, 2004) |
| 77 | Ballygisheen Bog | Lowland Blanket Bog | Kerry | 69500 | 81400 | TTP & spores excl. peatland taxa | (Cole & Mitchell, 2003) |
| 78 | Dromteewakeen | Blanket Bog | Kerry | 76000 | 81000 | TP excl. peatland taxa | (Lynch, 1981) |
| 79 | Dromatouk | Blanket Bog | Kerry | 95000 | 71000 | TP excl. peatland taxa | (Lynch, 1981) |
| 80 | Maughanasilly | Blanket Bog | Cork | 105000 | 58000 | TP excl. peatland taxa | (Lynch, 1981) |
| 81 | Cashelkeelty | Blanket Bog | Kerry | 75000 | 57000 | TP excl. peatland taxa & *Salix* | (Lynch, 1981) |
| 82 | Cullenagh | Blanket Bog | Cork | 116000 | 53000 | TP excl. peatland taxa | (Lynch, 1981) |
| 83 | Cadogan's Bog | Lowland Blanket Bog | Cork | 89842 | 34269 | TTP | (Mighall *et al.*, 2004) |
| 84 | Mount Gabriel | Upland Blanket Bog | Cork | 93000 | 34000 | TTP | (Mighall & Lageard, 1999) |

TP: Total Pollen; TTP: Total Terrestrial Pollen; AP: Arboreal Pollen; -: Not Given

### 2.3.3 Data Analysis and Mapping

The mean *Pinus* pollen frequency across all sites and its standard error were calculated for each time interval. Due to the non-normal distribution of the data, the non-parametric Spearman's rank correlation coefficient was calculated for site attributes and *Pinus* pollen frequencies at each time interval using Data Desk 6.1 (Velleman, 1997).

Isopoll maps were compiled with ArcView GIS 3.2 and its Spatial Analyst extension (ESRI, 1999) using the Inverse Distance Weighting method of spatial interpolation. This method was chosen over kriging as it is user-friendly, does not require prior knowledge of the data and is well suited to the production of maps for illustrative purposes (Fortin & Dale, 2005). Weighting power determines how quickly interpolated values decline with distance from an observed peak. Low powers, such as 1, produce a rapid decline while high powers, such as 4, produce a slower decline. Weighting power was set at 3 for the interpolation models of *P. sylvestris* pollen frequency, so that the influence of pollen peaks declined fairly slowly with distance from the site. This allowed for the high dispersal ability of *P. sylvestris* (Bradshaw, 1981) and the relatively large, regional pollen source areas of the sequences used (Jacobson & Bradshaw, 1981). Nearest neighbours determine how many surrounding data points are used in the interpolation of a value for any given point. In a similar analysis of a dataset of 34 sites, Perrin (2003) found that 12 (35%) was an appropriate number of nearest neighbours, with other settings resulting in either undue influence of distant sites or gaps in the interpolated surface. In this study, the number of sites with available data varied with each time interval (Fig. 2.2), so the 35% proportion was applied. A non-linear scale was applied to the contour classes to provide a clearer representation of low *Pinus* pollen frequencies. The 5% and 20% contour classes represent the 5% and 20% critical pollen percentages (Bennett, 1984, 1995). The sites used in the calculation of interpolated pollen frequencies at each time interval are mapped

with a black dot. The purple monochromatic colour scheme was selected to represent pollen frequencies as it provides good contrast in both colour and greyscale, without obscuring the location of the sites.

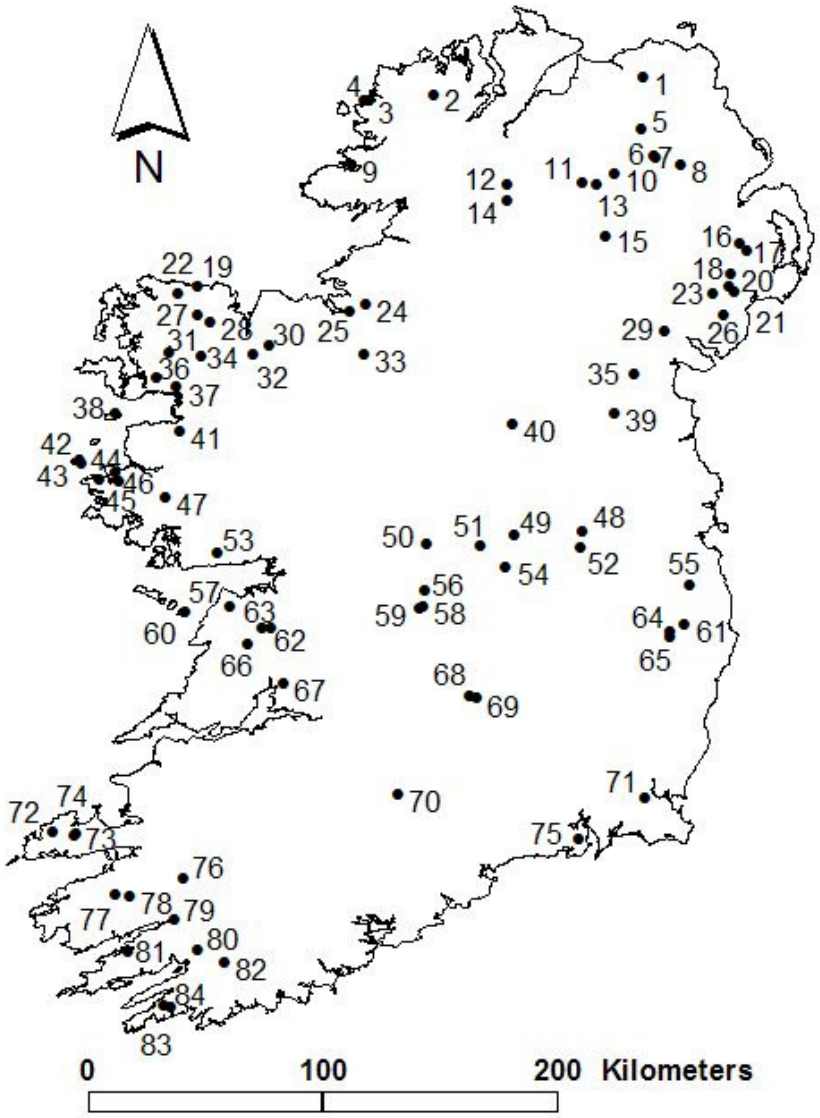



Figure 2.1. Location map of the 84 pollen sampling sites used in the compilation of isopoll maps, listed in Table 2.1.

### 2.3.4 Map Interpretation and Sources of Error

Huntley and Birks (1983) gave an overview of issues associated with the interpretation of isopoll maps. The accuracy of the isopoll maps presented here was dependent upon the quality and interpretation of the data, particularly at low frequencies, and on the validity of the assumptions made during spatial interpolation. Several sources of error should be considered:

1. The geographical spread of data points was uneven (Fig. 2.1, Figs. 2.3 a-x) and should be considered when comparing interpolated pollen frequencies in areas where sites were sparse with those where more sites were available.
2. The number of data points mapped varied with time interval, from 21 at 11,500 cal BP to 63 at 2000 cal BP (Fig. 2.2), due to differences in the timespans covered by the pollen sequences. This must be considered when comparing maps from different time intervals.
3. Many of the sequences examined exhibited low sediment accumulation rates during the early Holocene, so dating precision during this period may be reduced. Some of the radiocarbon dates used may be in error. When constructing calibrated age-depth curves, dates that were obviously in error were omitted i.e. inverted dates. In any case, the 500 year time interval between the maps is greater than twice the typical standard deviation of an early postglacial radiocarbon date (± 100 years) (Bennett, 1990), so pollen events should appear within the correct time interval. In addition, the large number of sites analysed should ensure that incorrect dates do not obscure wider patterns.
4. There are numerous ways in which pollen sample contamination may occur but the most likely in this case would be the contamination of sediment lacking *Pinus* pollen with either younger or older sediment containing abundant *Pinus* pollen. Since about 1970, improved awareness of field contamination has ensured the minimisation of this source of error

(Bennett, 1990). Almost all of the studies included in this analysis were conducted since then, so sample contamination is unlikely to be a significant source of error, although inwash of eroded peat containing *Pinus* pollen may be an issue in sequences from upland lakes (Bradshaw & McGee, 1988; Leira *et al.*, 2007).

5. Some variation exists in the pollen sum calculations used in the pollen sequences (Table 2.1). Most sequences used a total terrestrial pollen sum excluding local taxa but sequences where total or arboreal pollen sums were used should be interpreted carefully as these may produce skewed *Pinus* pollen frequencies. One site, Clonsast Bog (Mitchell, 1956), was excluded as its total arboreal pollen sum produced extremely high *Pinus* values, obscuring patterns in the midlands for much of the Holocene. Otherwise, the large number of sites analysed should ensure that differing pollen sum calculations do not obscure wider patterns.
6. As previously described, *Pinus* pollen representation factors are complex. *Pinus* pollen was generally identified to genus level which, in Ireland, is assumed to represent a single species, *P. sylvestris*. However, the 0 cal BP interval post-dated the introduction of non-native *Pinus* species to Ireland, and may include pollen of *P. contorta* etc., as noted at site 25 (Croaghan East) (Dwyer, 1995).

In light of these considerations, the isopoll maps and interpolated pollen frequencies were interpreted conservatively and at the broad landscape scale. Changes in *Pinus* pollen frequencies at individual sites were generally ignored in favour of wider, spatially coherent patterns. The 20% critical pollen percentage was not used. The 11,500 cal BP isopoll map (Fig. 2.3a) suggested that the background *Pinus* pollen frequency in Ireland prior to the arrival of *Pinus* was in the 0.1 to 4.9% range, so the 5% critical pollen percentage was adopted to give a rough indication of the presence of *P. sylvestris* around a palaeoecological site. When available, data on *Pinus* macrofossils and stomata were used as a more accurate indication of local presence.

## 2.4 Results and Discussion

Mean *Pinus* pollen frequencies across all sites increased steadily from 3.3% at 11,500 cal BP, accelerating from 10,500 cal BP onwards (Fig. 2.2). Peak frequencies were achieved at 7500 cal BP, reaching 17.6%. *Pinus* then began to decline, accelerating between 6500-6000 and 5000-3500 cal BP, and reached a minimum of 1.6% at 2500 cal BP. Small standard error values during this period indicated consistently low *Pinus* pollen frequencies among the sites analysed. From this point on, small, gradual increases were observed. A substantial increase appeared at 0 cal BP, when the mean frequency reached 8.6%. When site 27 (Croaghan East) was omitted, due an unusually high value (86%) attributed to surrounding plantations of *P. contorta* (Dwyer, 1995), the mean *Pinus* pollen frequency for 0 cal BP was 7.0% ± 1.5. Figure 2.2 illustrates well defined phases in the postglacial dynamics of *Pinus* in Ireland, which provide a temporal framework for the description and interpretation of the associated isopoll maps. A series of significant correlations occurred between *Pinus* pollen frequencies and altitude, eastings and northings (Irish grid) at various intervals during the Holocene (Table 2.2) and are discussed below.

### 2.4.1 Isopoll Maps (Figs. 2.3 a-x, Appendix 2.1)

*11,500 – 11,000 cal BP Absence (Figs. 2.3 a-b)*

*Pinus* is not thought to have colonised Ireland by this time and this is largely supported by the isopoll maps. In accordance with the revised 5% critical pollen percentage (Bennett, 1995), the 0.1-4.9% *Pinus* pollen frequencies observed through most of Ireland probably represent 'background' levels of *Pinus* pollen, due to long distance transport. Figure 2.2 shows that *Pinus* pollen frequencies during the early Holocene were higher than those during the later period of

extirpation. This is probably due to the exaggeration of the long distance component at a time when indigenous pollen production was relatively low and vegetation cover relatively sparse. Values increased slightly over time as the *Pinus* migration approached Ireland (Huntley & Birks, 1983).

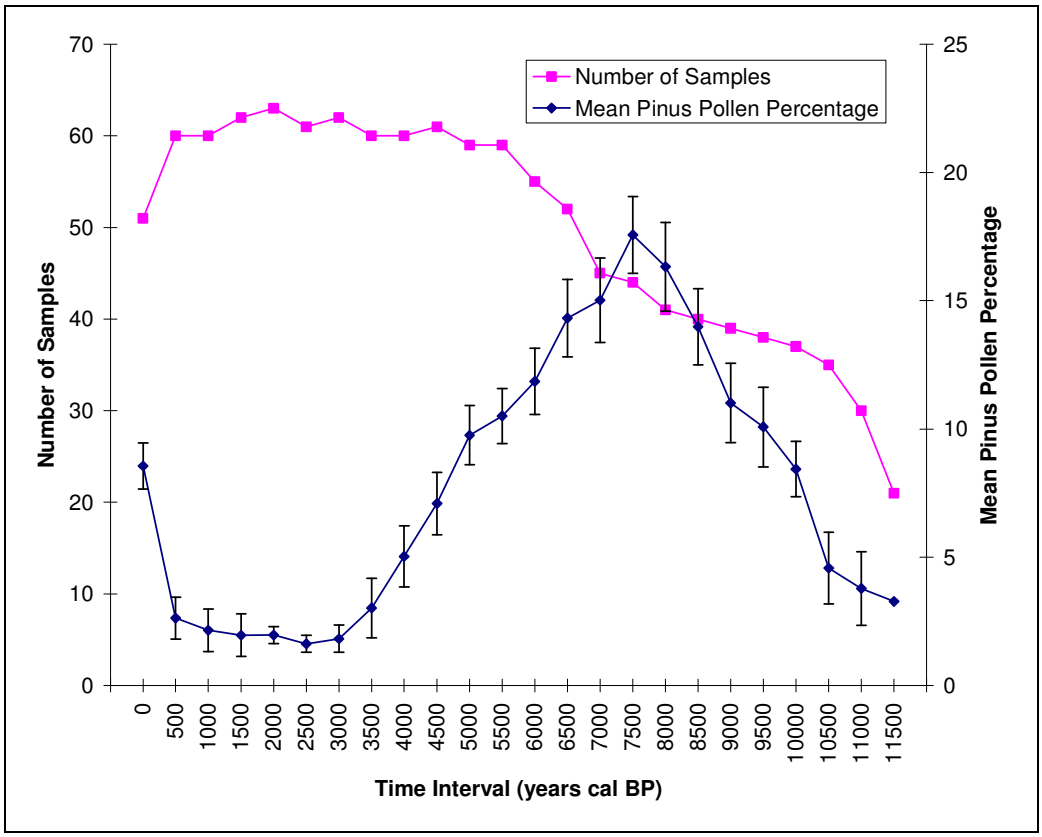



Figure 2.2. Number of pollen sequences analysed and mean *Pinus* pollen frequency (± standard error) for each time interval.

A few exceptions are observed where *Pinus* pollen frequencies exceed 5%. In western Ireland, the radiocarbon dates for the early postglacial *Juniperus* peak at sites 34 and 36 appear to be too old (12,210 ± 70 BP and 10,530 ± 100 BP respectively) (Browne, 1986) relative to other sites in the County Mayo area. If this is the case, the observed *Pinus* pollen frequencies relate to a slightly later time period. The high frequencies observed in the south at site 70 may be an artefact of the pollen sampling properties of this high altitude corrie lake (476 m, Leira *et al.*,

unpublished). It must be emphasised that these exceptions are not therefore thought to represent the presence of *Pinus* in Ireland at this time.

*10,500 – 7500 cal BP Arrival, expansion, peak (Figs. 2.3 c-i)*

At 10,500 cal BP, increased *Pinus* pollen frequencies were recorded at sites 37 (Lough Aisling, 16.5%), 63 (Gortlecka, 17.5%) and 43 (Church Lough, 7%), where values were previously zero or less than 5% (Fig. 2.3c). This suggests that *P. sylvestris* colonised western Ireland by 10,500 cal BP, with the earliest populations occurring in County Mayo, the Burren area of County Clare and perhaps on Inisbofin. This finding is corroborated by the first appearance of *Pinus* macrofossils at around this time in the Gortlecka sequence from the Burren (Watts, 1984a). Mitchell's (2006) isochrone maps support this timing of arrival, but not the direction of migration. They suggest that *Corylus* migrated to Ireland by crossing the Irish Sea, while *Pinus*, *Ulmus* and *Quercus* migrated from the south via the Celtic Sea. The isopoll map (Fig. 2.3c) implies that *Pinus* first colonised the west of Ireland. Consequently, the accepted hypothesis in which *Pinus* first arrived in south-western Ireland (Mitchell & Ryan, 1997; Mitchell, 2006) may need to be reviewed.

Bennett (1984) interpreted the very early presence of *P. sylvestris* in western Ireland as a possible indication that the British and Irish populations expanded from separate glacial refugia. The term "cryptic refugia" refers to areas with sheltered topography and buffered, stable local microclimates where isolated populations persisted during glacial stages, but were too localized or small to be detected by conventional palynological techniques (Birks, 1989; Stewart & Lister, 2001). Furthermore, putative source populations cannot be identified by molecular techniques as the presumed extirpation of Irish *Pinus* populations precludes such a comparison (Sinclair *et al.*, 1998). Discussion on the source of this early western population is therefore beyond the scope of this study.

Table 2.2. Spearman rank correlation coefficients for altitude, location (Irish grid) and *Pinus* pollen frequencies at each time interval.

| | Altitude | Eastings | Northings | n |
|---|---|---|---|---|
| Eastings | 0.132 | - | - | 84 |
| Northings | -0.176 | 0.436*** | - | 84 |
| *Pinus* Pollen Frequencies | | | | |
| 11,500 cal BP | 0.392 | -0.277 | -0.106 | 21 |
| 11,000 cal BP | 0.474* | -0.207 | -0.305 | 30 |
| 10,500 cal BP | -0.236 | -0.316 | -0.284 | 35 |
| 10,000 cal BP | -0.151 | -0.215 | -0.258 | 37 |
| 9500 cal BP | -0.076 | -0.304 | -0.307 | 38 |
| 9000 cal BP | -0.012 | -0.238 | -0.336* | 39 |
| 8500 cal BP | 0.048 | -0.198 | -0.401* | 40 |
| 8000 cal BP | 0.164 | -0.091 | -0.240 | 41 |
| 7500 cal BP | 0.199 | -0.088 | -0.266 | 44 |
| 7000 cal BP | 0.431** | -0.166 | -0.120 | 45 |
| 6500 cal BP | 0.285* | -0.402** | -0.155 | 52 |
| 6000 cal BP | 0.197 | -0.401** | -0.307* | 55 |
| 5500 cal BP | 0.157 | -0.428** | -0.117 | 59 |
| 5000 cal BP | -0.017 | -0.366** | -0.047 | 59 |
| 4500 cal BP | -0.129 | -0.374** | -0.137 | 61 |
| 4000 cal BP | -0.107 | -0.144 | -0.036 | 60 |
| 3500 cal BP | -0.051 | -0.180 | -0.030 | 60 |
| 3000 cal BP | -0.168 | -0.165 | 0.010 | 62 |
| 2500 cal BP | -0.238 | -0.130 | 0.070 | 61 |
| 2000 cal BP | -0.214 | -0.086 | -0.032 | 63 |
| 1500 cal BP | -0.175 | 0.044 | 0.007 | 62 |
| 1000 cal BP | -0.218 | -0.050 | 0.169 | 60 |
| 500 cal BP | -0.020 | 0.048 | 0.030 | 60 |
| 0 cal BP | -0.143 | 0.334* | 0.225 | 51 |

Statistically significant correlations are indicated: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

From 10,000 cal BP, consistent patterns began to emerge over larger areas. Increases in *Pinus* pollen frequencies continued at established sites and were initiated at neighbouring sites where values were previously low (Fig. 2.2, Fig. 2.3 d-i). In the Burren, sites 63 and 66 displayed consistent frequencies of 21.5 and 20.0% respectively, while in County Mayo, sites 36 and 37 displayed frequencies of 30.0 and 32.5% respectively. This reflects the proliferation of *Pinus* and its expansion into neighbouring areas. *Pinus* pollen frequencies in the south-west were somewhat erratic but increased values were recorded there for the first time at 10,000 cal BP. *Pinus* appeared to migrate rapidly eastwards initially, with elevated values being recorded in the midlands and east around 10,000 cal BP, and

more slowly northwards, with elevated values being recorded in western Donegal at 9000 cal BP and eastern Ulster at 8500 cal BP. The significant negative correlations between *Pinus* pollen frequencies and northings from 9000-8500 cal BP (Table 2.2) reflect the fact that *Pinus* was more established in the south at that time. Its average rate of spread in Ireland has been estimated at 250-360 m year$^{-1}$ (Bennett, 1984; Mitchell, 2006). Mitchell's (2006) isochrone map supports the timing of arrival but not the direction of migration in the midlands and east, while conversely supporting the direction but not the timing in Donegal and eastern Ulster. The disparities between the isochrone and isopoll maps may be related to their differing time scales and purposes. The isochrone map records the timing of the arrival of *Pinus* in uncalibrated years BP, specifically depicting migration patterns. The isopoll maps record *Pinus* pollen frequencies at fixed intervals in calibrated years BP and are not specifically intended to show the exact timing of pollen stratigraphic events, such as the empirical or rational limit as defined by Smith and Pilcher (1973).

Froyd (2005) highlighted differences in the *Pinus* records arising from pollen and stomatal evidence. In western Donegal, the first records of stomata demonstrate the local presence of *Pinus* at site 9 (Lough Mullaghlahan) at 9550 cal BP, despite corresponding *Pinus* pollen frequencies of 2.8%, site 4 (Altar Lough) at 9380 cal BP and site 3 (Lough Nabraddan) at 8600 cal BP (Fossitt, 1994). This pattern is consistent with a northward migration, but demonstrates some departures from the timing suggested by the isopolls, which were based solely on pollen data.

Relatively high *Pinus* pollen frequencies of at least 10% across most of Ireland, with large areas exceeding 20% (Fig. 2.3h), suggest that the establishment of forests with a significant component of *Pinus* was complete by about 8000 cal BP, as observed by Bennett (1984). Indeed, *Pinus* was the dominant arboreal pollen type in almost all western and most upland study sites for at least part of the early Holocene (Bennett, 1984; Bradshaw & Browne, 1987). The isopoll maps are consistent with this distribution, which probably arose because of competitive

interactions. *Quercus*, *Ulmus* and *Corylus* are thought to have dominated lowland central and eastern base-rich soils, while *Pinus* was limited to raised bogs, river valleys, uplands and western areas including the limestone pavement of the Burren (Bennett, 1984; Watts, 1984a; Bradshaw & Browne, 1987). *Pinus*' tolerance of nutrient deficient soils and, in the case of the Burren, drought, lent it a competitive advantage in these habitats (Carlisle & Brown, 1968; Bennett, 1984).

The origin of many of the pollen sequences analysed (Table 2.1) coincides closely with the habitat preferences of *Pinus* at this time. However, sites 40 (Ballywillin Crannóg, Lough Kinale) and 49 (Cornaher Lough) are both lowland, midland lakes over limestone bedrock. These sites showed low *Pinus* pollen frequencies during this period, indicating that *Pinus* was not a significant component of the forests in this region. Higher *Pinus* values were observed in mountainous areas such as Connemara and the Nephin Begs in the west, the Wicklow Mountains in the east and the Galtee Mountains in the south and at raised bogs such as sites 5 (Fallahogy) in the north and 51 (Clara Bog) in the midlands. The shortage of sequences from central and eastern lowland sites on base-rich substrates is likely to have resulted in some overestimation of the interpolated pollen frequencies for these areas when nearby sequences have been derived from raised bog or upland sites.

There appears to have been a short period of relative stability from 8500-7500 cal BP (Figs. 2.3 g-i), where little widespread change occurred apart from gradual increases in the north and fluctuations at individual sites elsewhere. Mean *Pinus* pollen frequencies achieved their Holocene maximum (17.6%) at 7500 cal BP (Fig. 2.2).

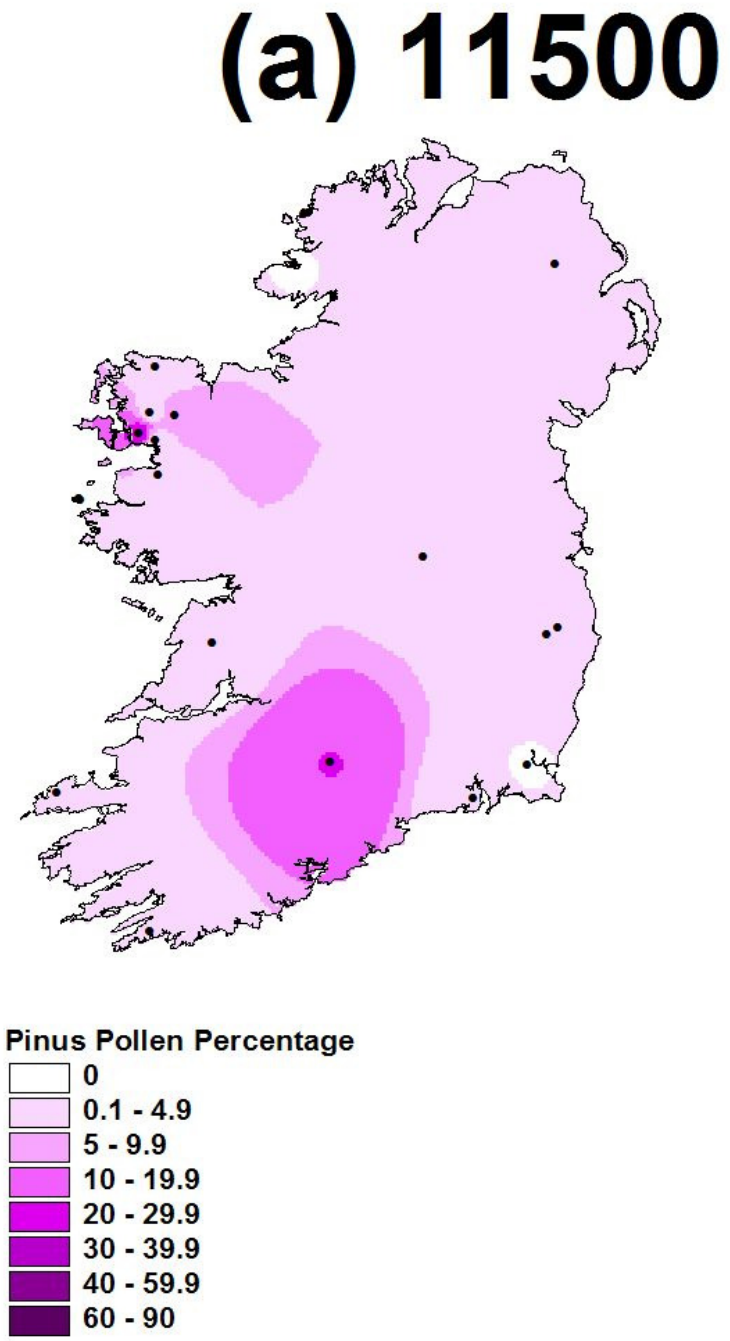
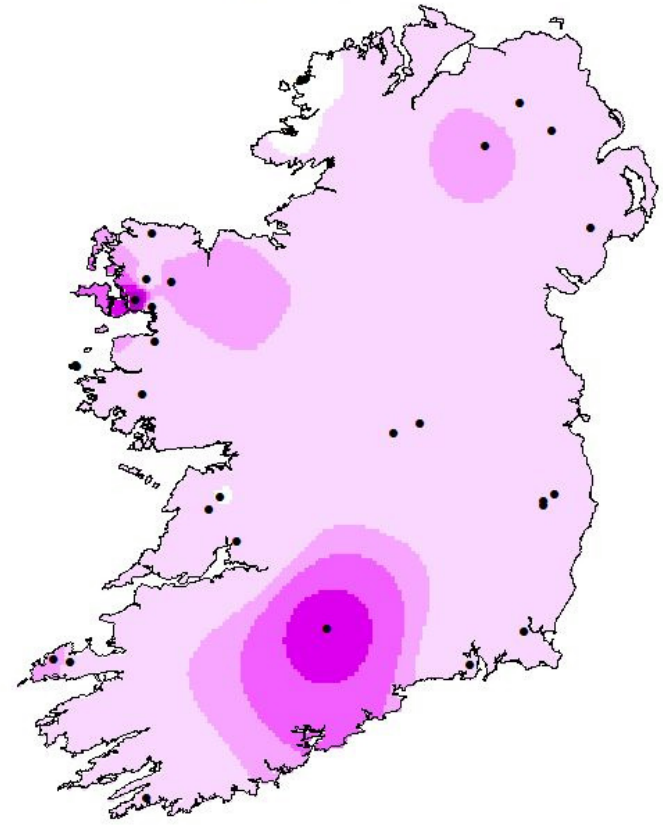



Figure 2.3 (a-x). Isopoll maps for *Pinus* in Ireland from 11,500-0 cal BP. Refer to Section 2.4.1 for detailed interpretation of pollen signals.

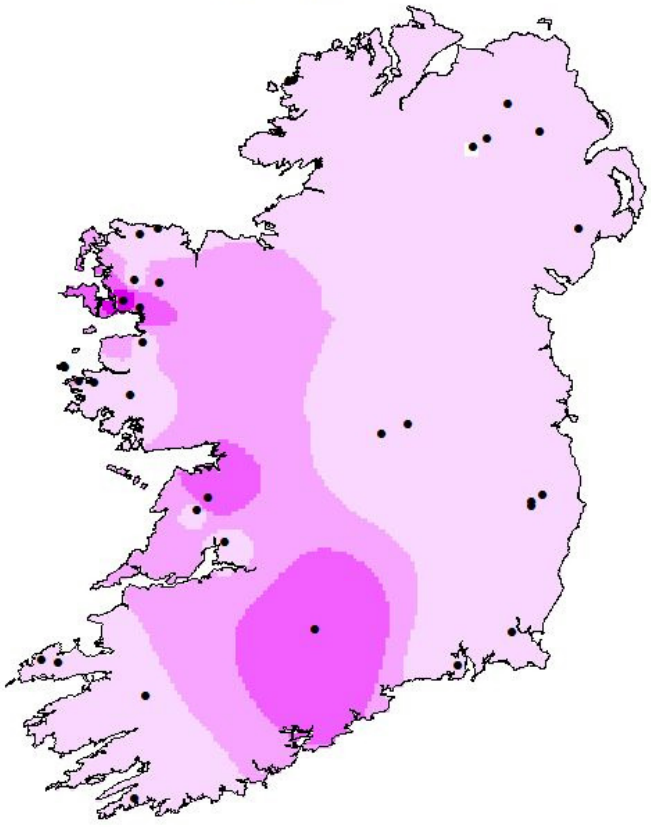
# (b) 11000



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

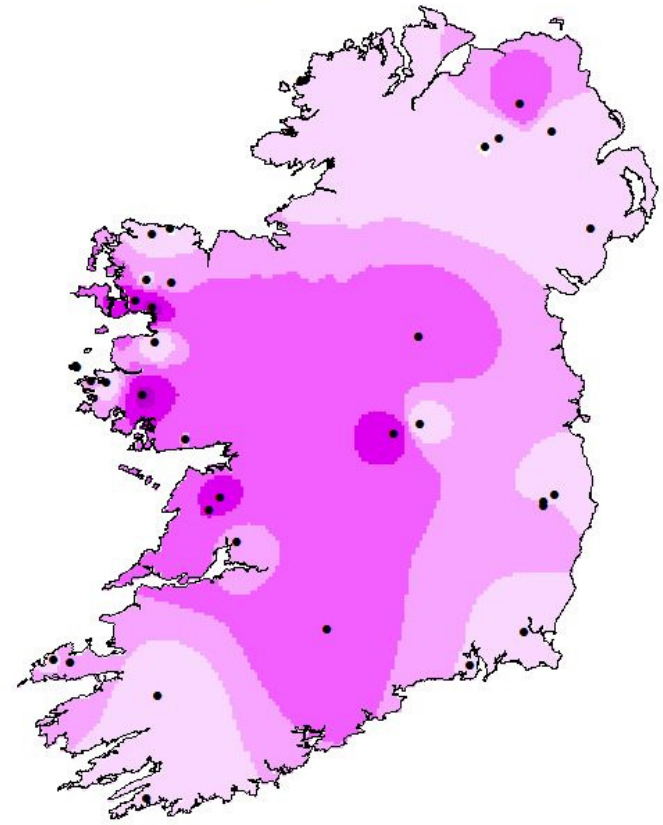
# (c) 10500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

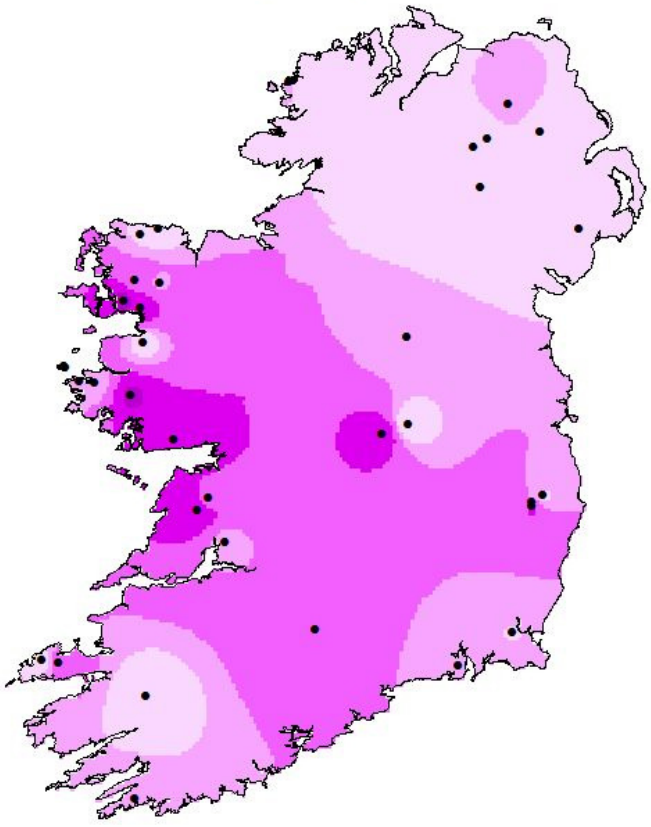
# (d) 10000



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

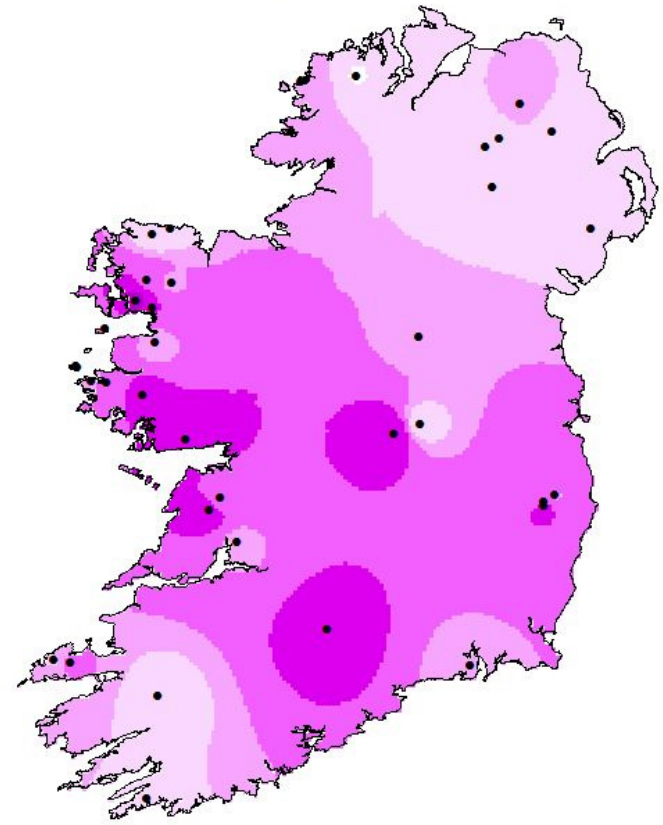
# (e) 9500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

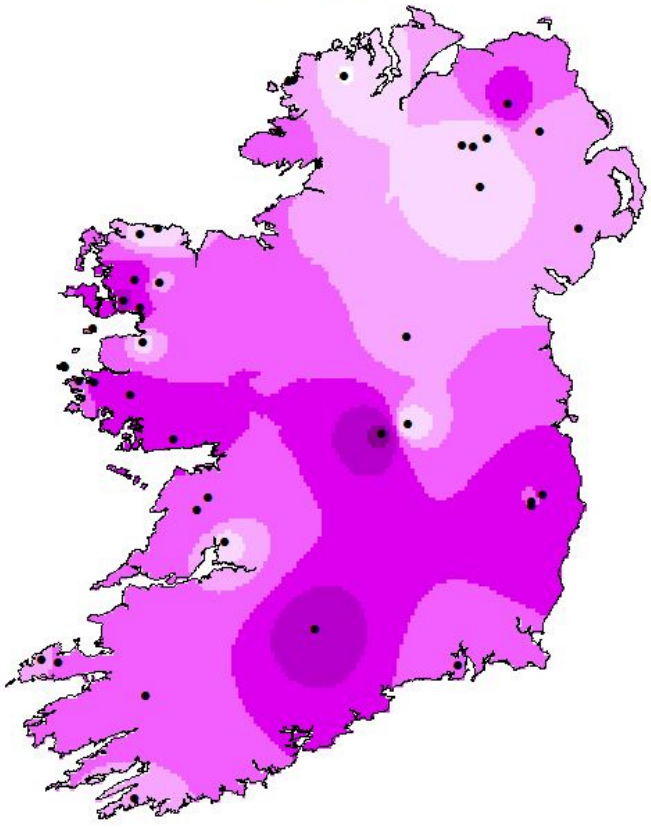
# (f) 9000



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

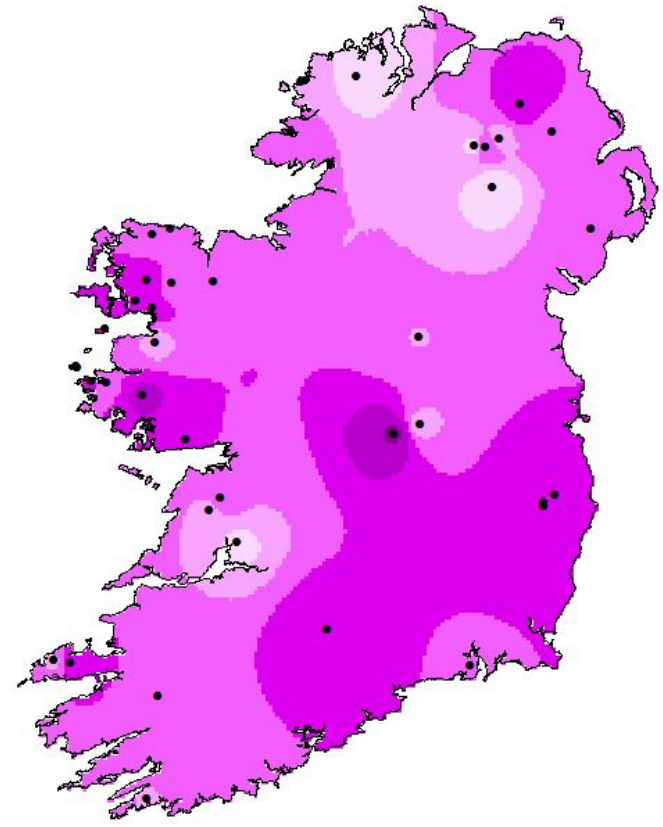
# (g) 8500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

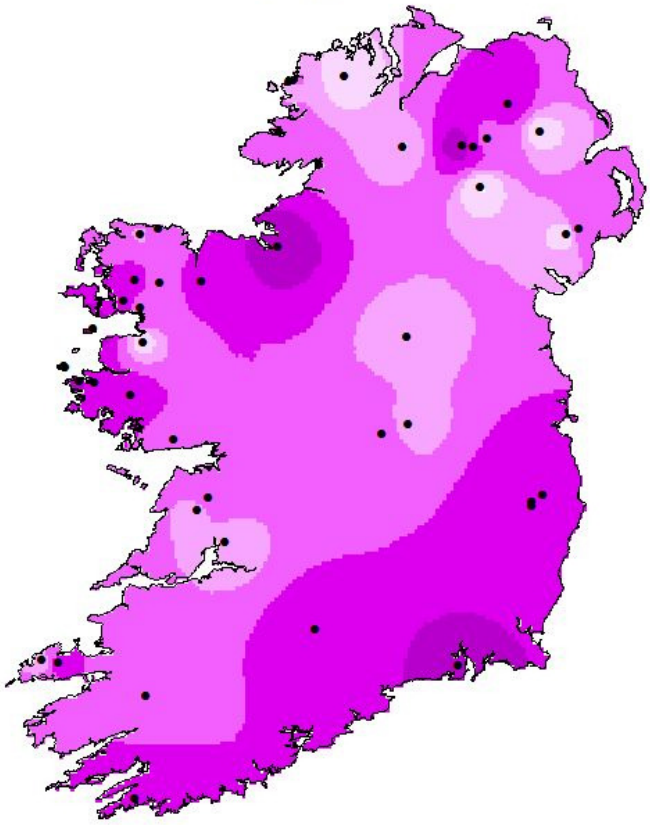
# (h) 8000



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

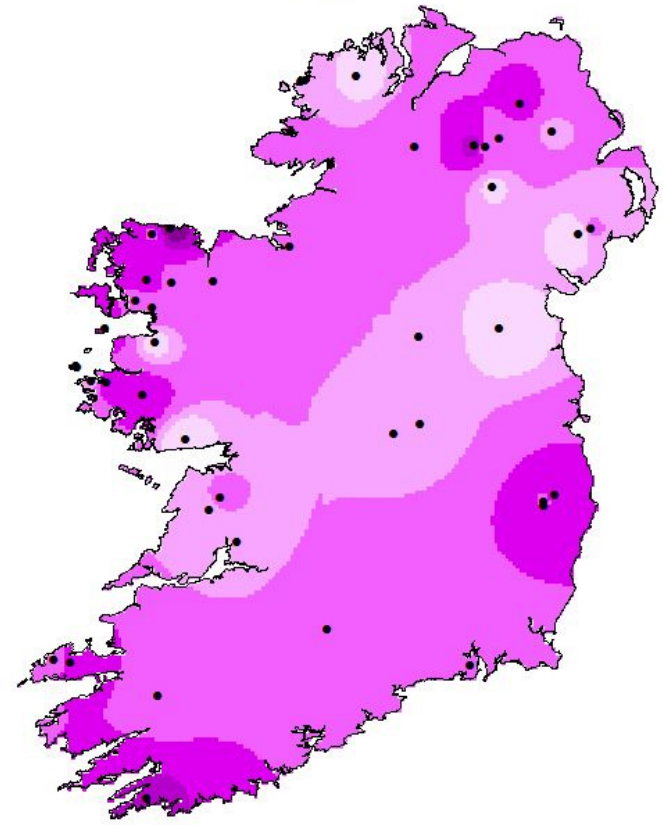
# (i) 7500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

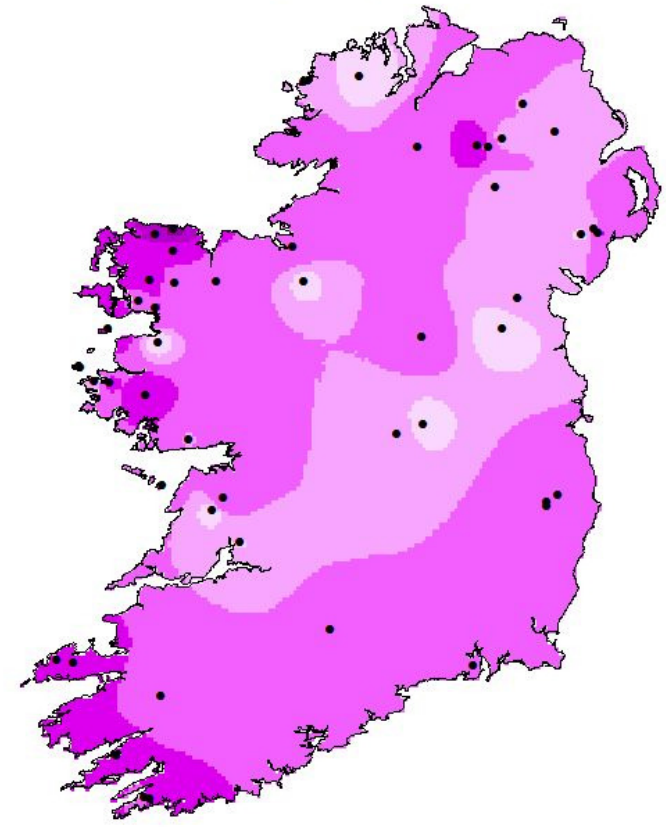
# (j) 7000



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

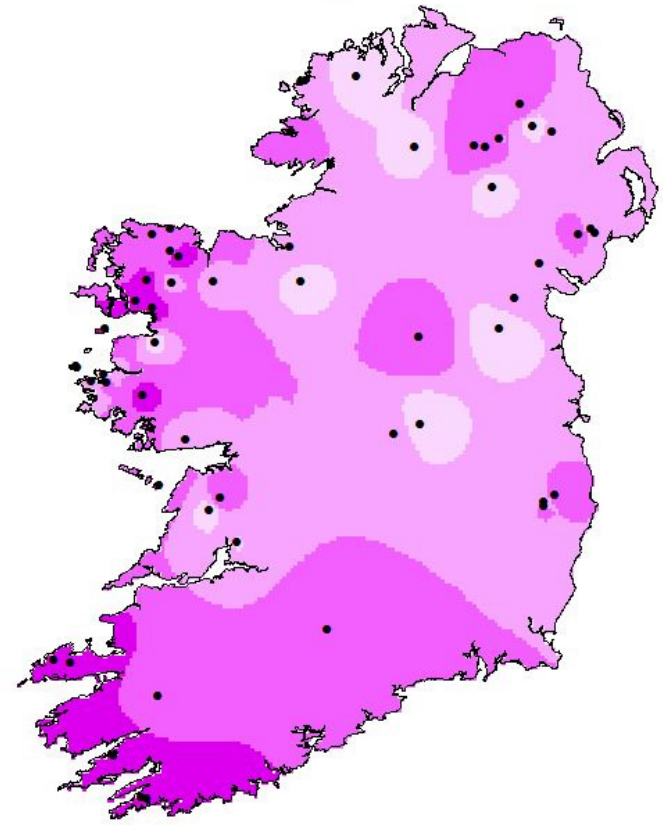
# (k) 6500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

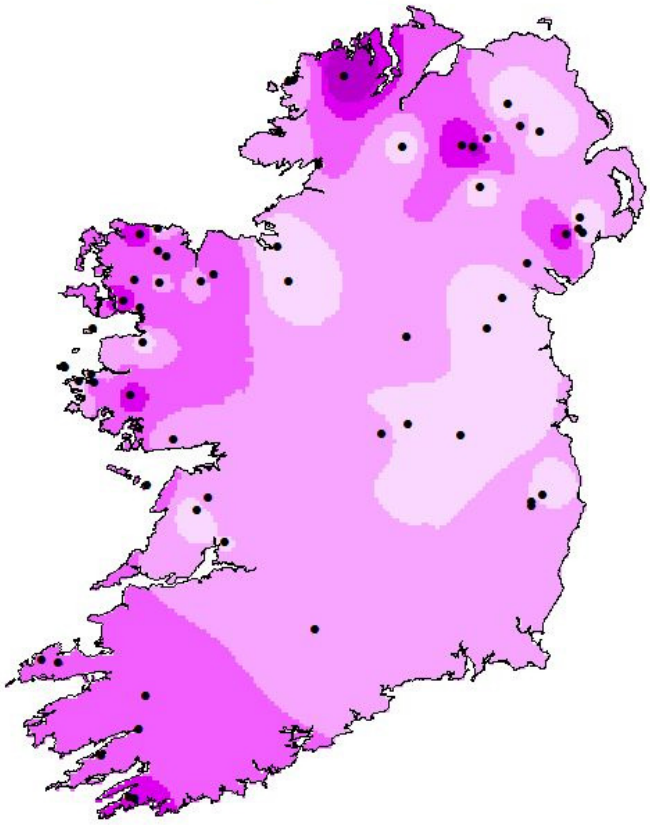
# (I) 6000



**Pinus Pollen Percentage**

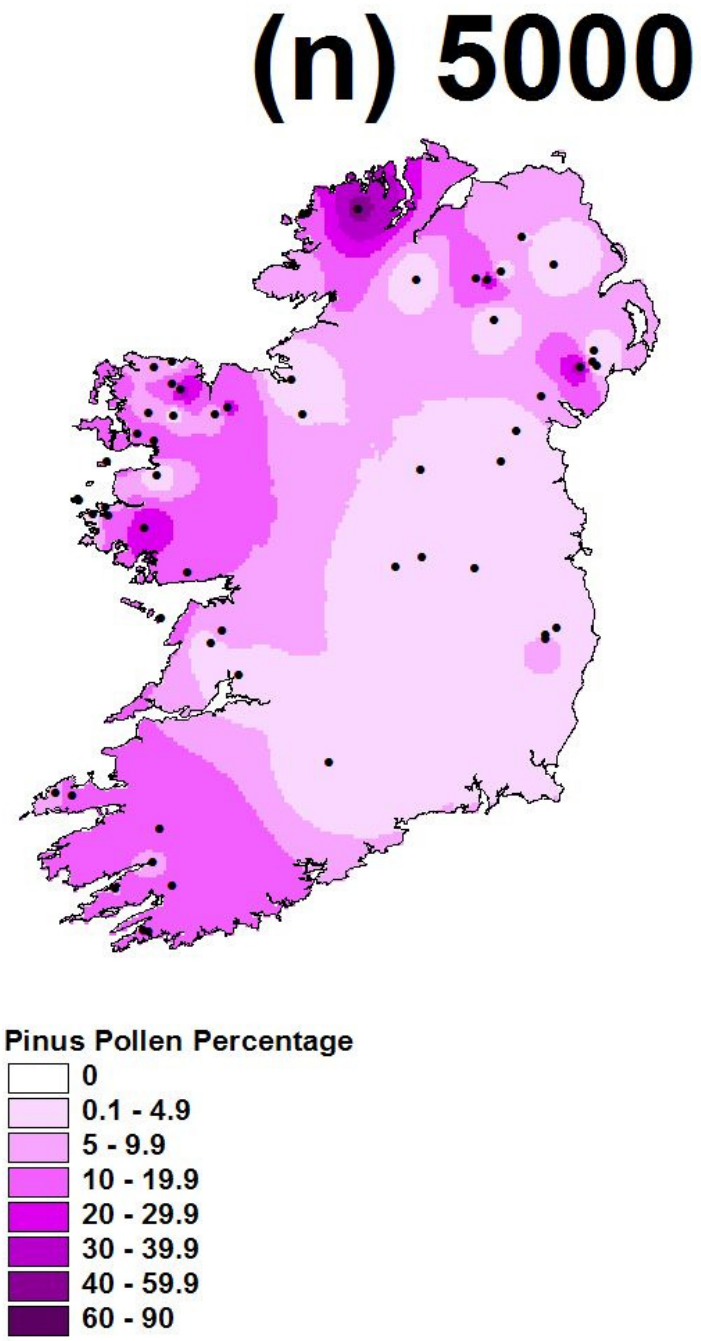
- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

# (m) 5500

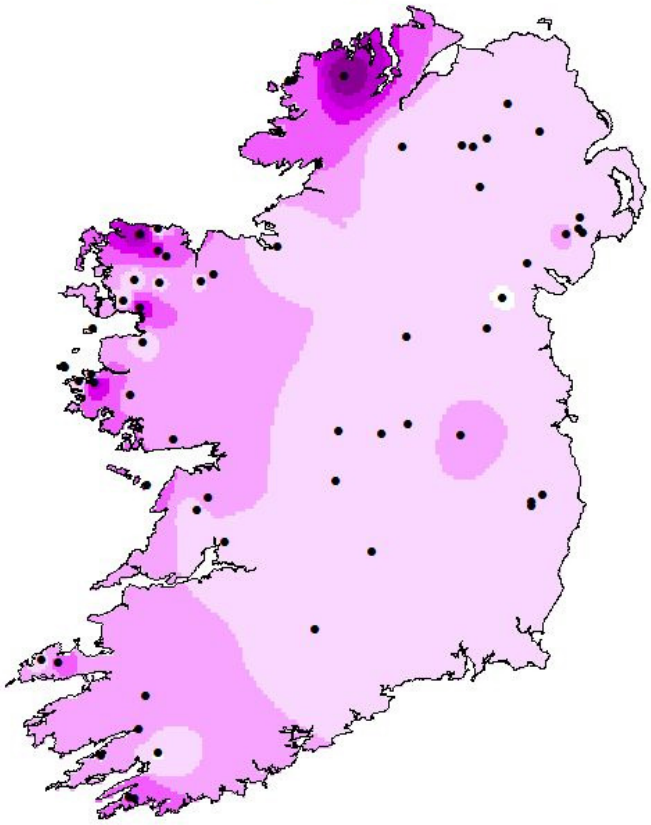


**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90


(n) 5000
Pinus Pollen Percentage
0
0.1 - 4.9
5 - 9.9
10 - 19.9
20 - 29.9
30 - 39.9
40 - 59.9
60 - 90

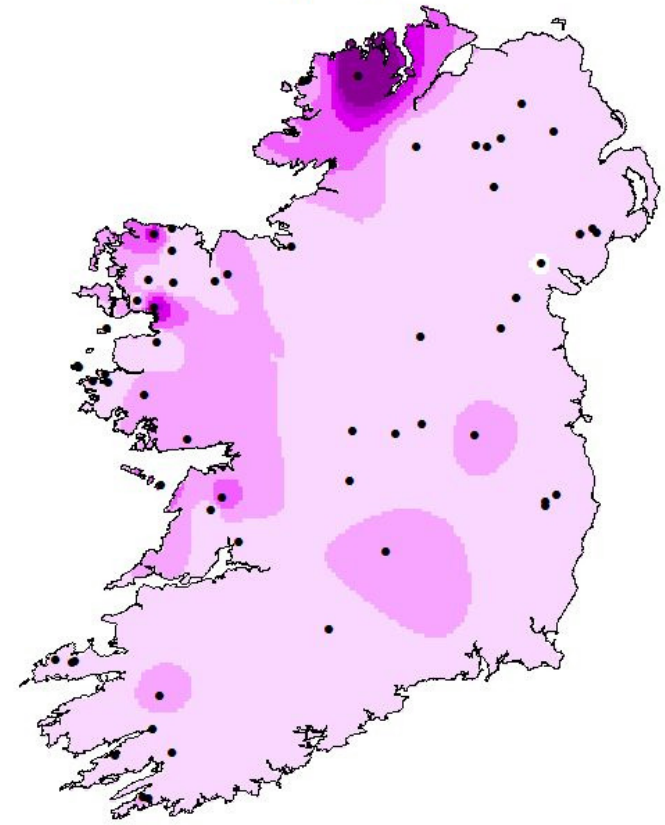
# (o) 4500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

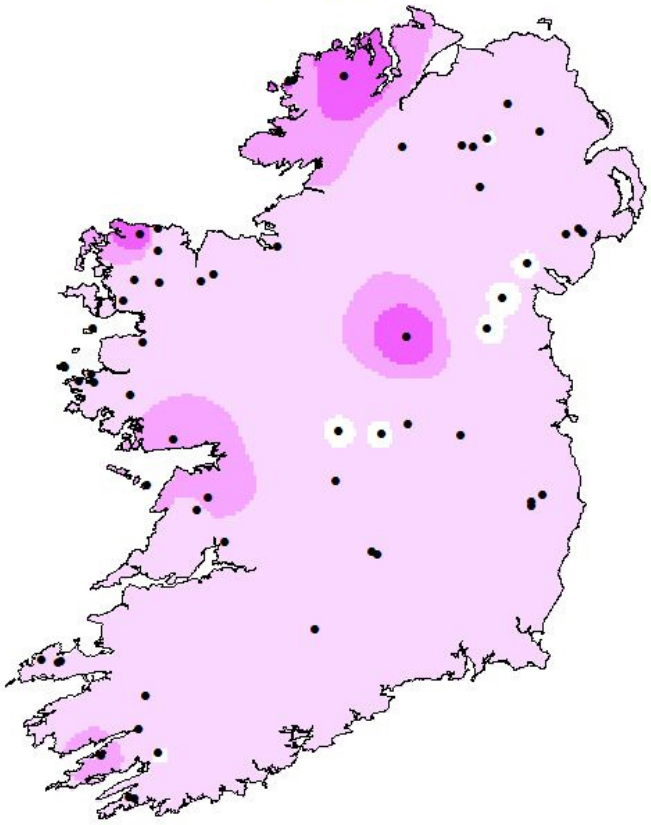
# (p) 4000



**Pinus Pollen Percentage**

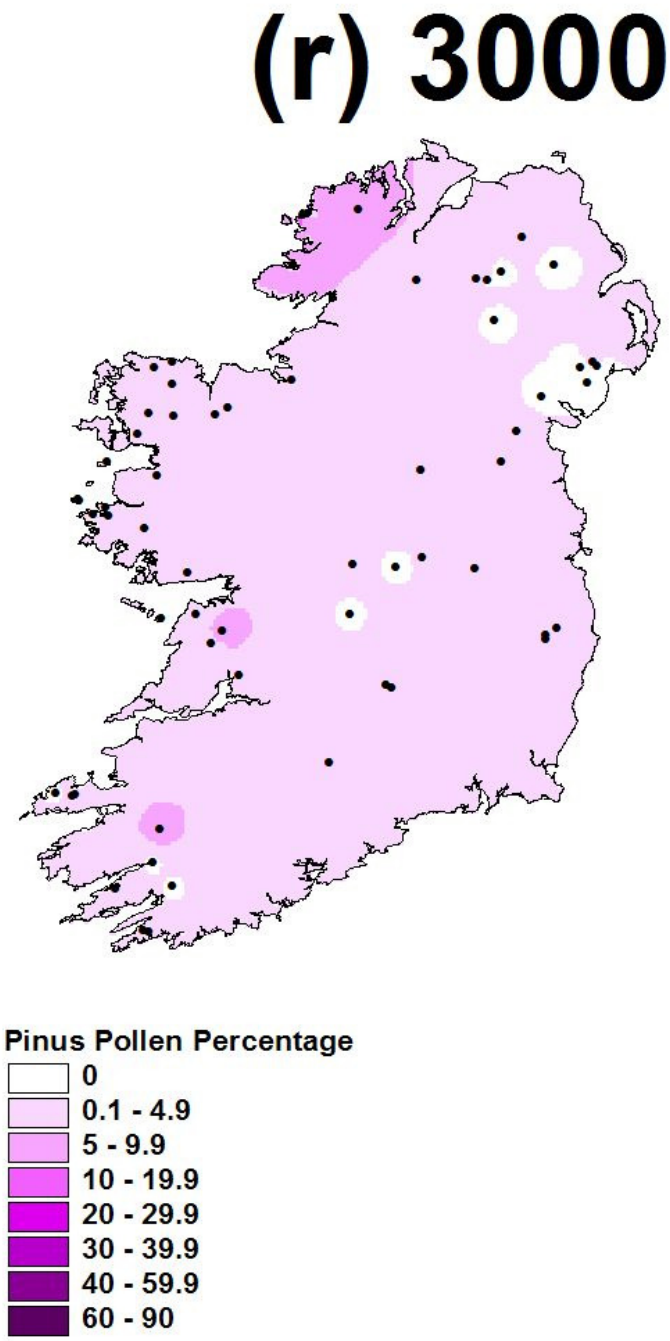
- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

# (q) 3500

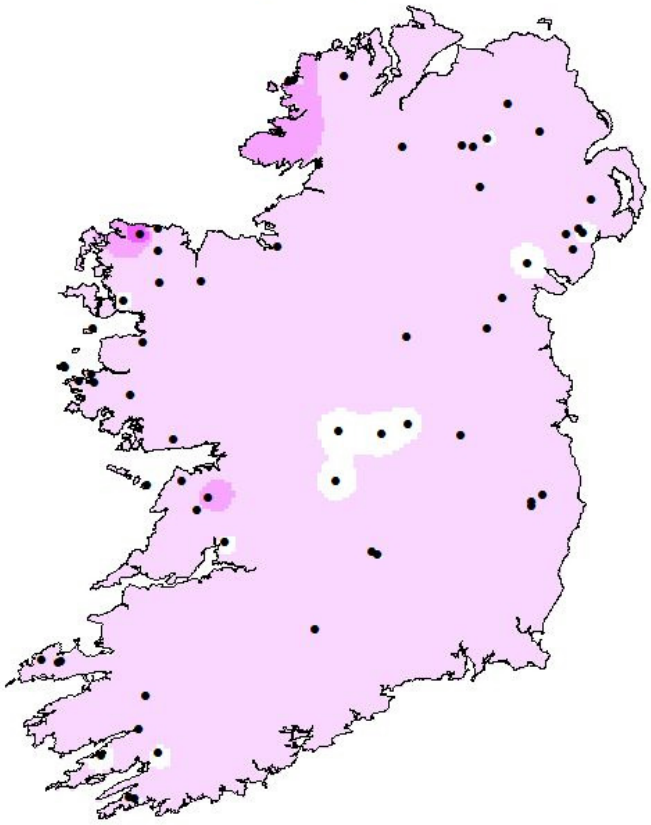


**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

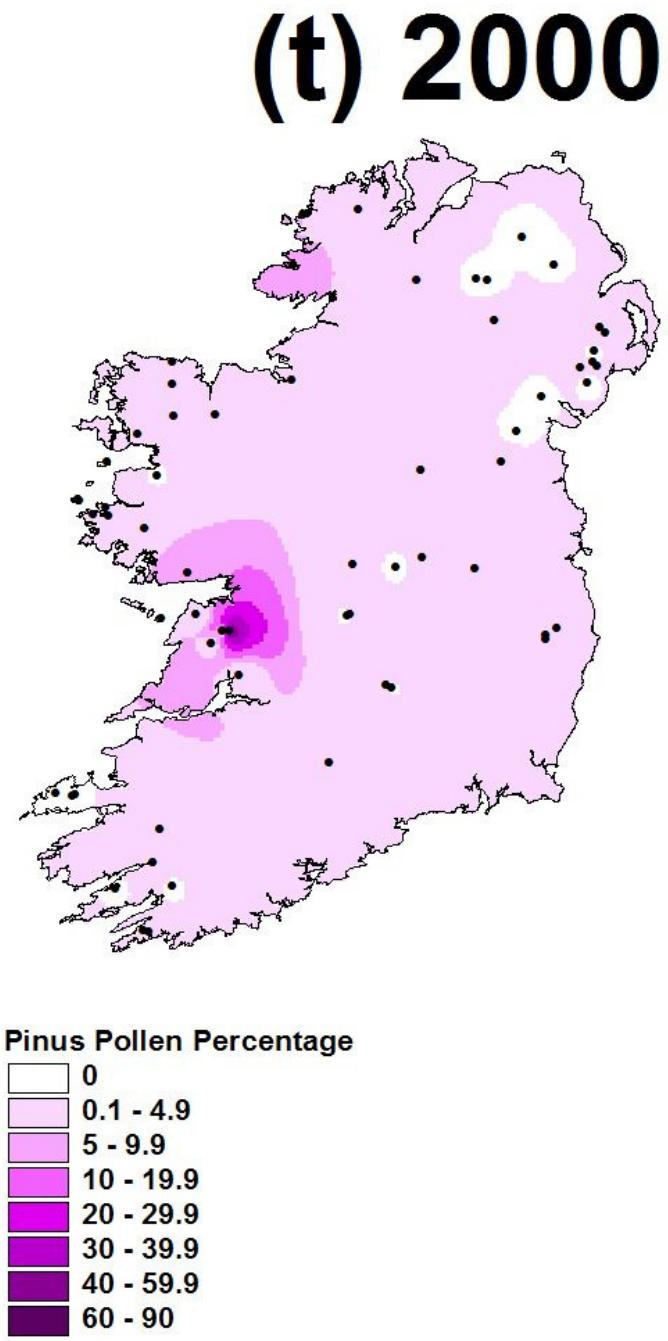

(r) 3000
Pinus Pollen Percentage
0
0.1 - 4.9
5 - 9.9
10 - 19.9
20 - 29.9
30 - 39.9
40 - 59.9
60 - 90

# (s) 2500

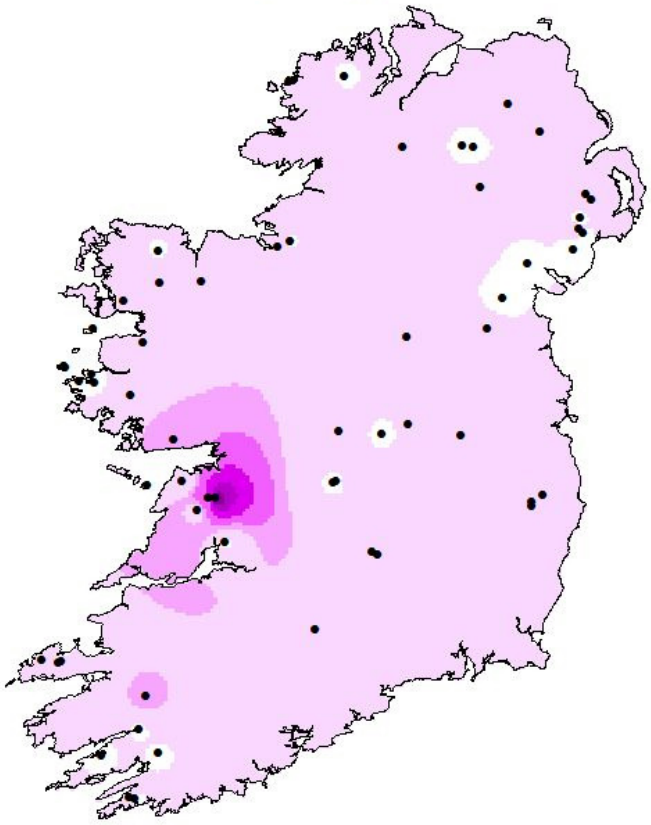


**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90


(t) 2000
Pinus Pollen Percentage
0
0.1 - 4.9
5 - 9.9
10 - 19.9
20 - 29.9
30 - 39.9
40 - 59.9
60 - 90

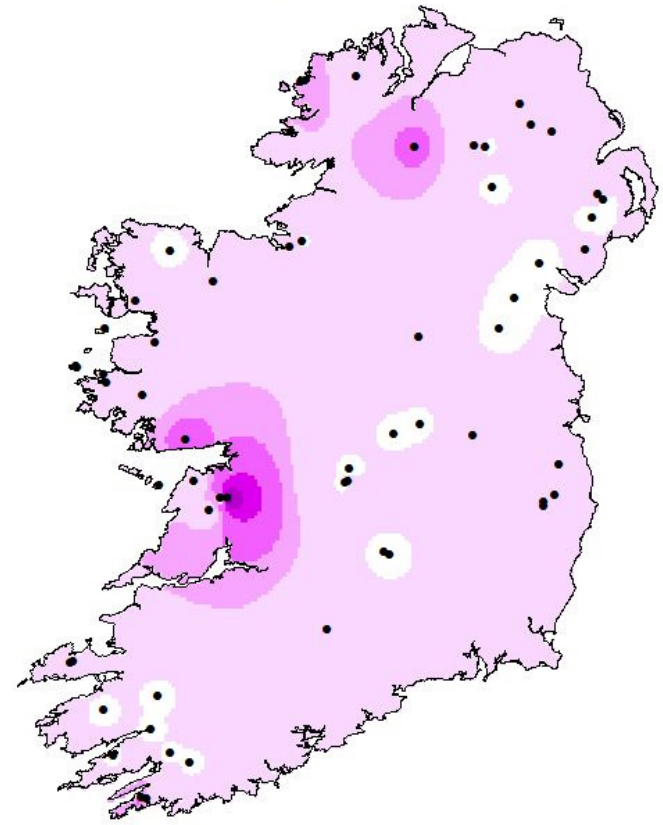
# (u) 1500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

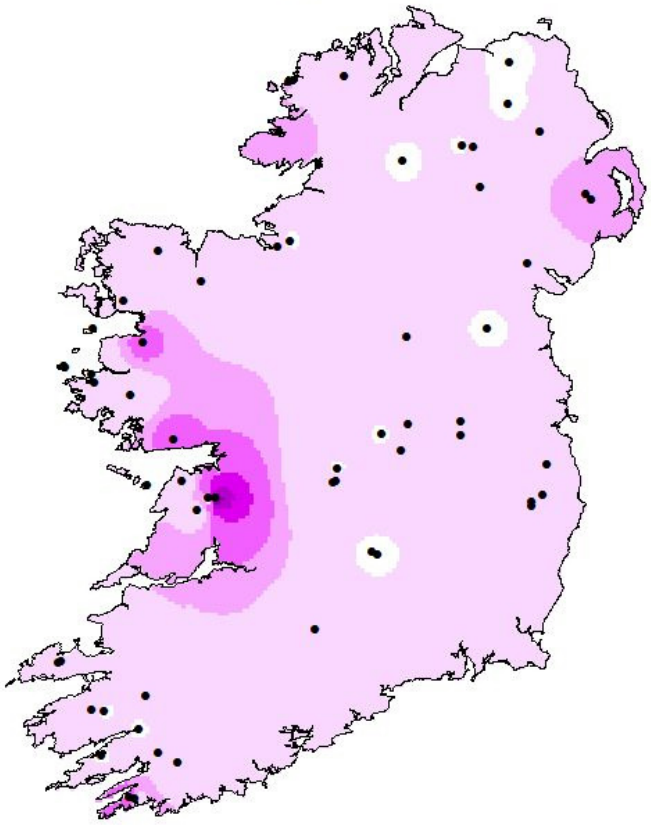
# (v) 1000



**Pinus Pollen Percentage**

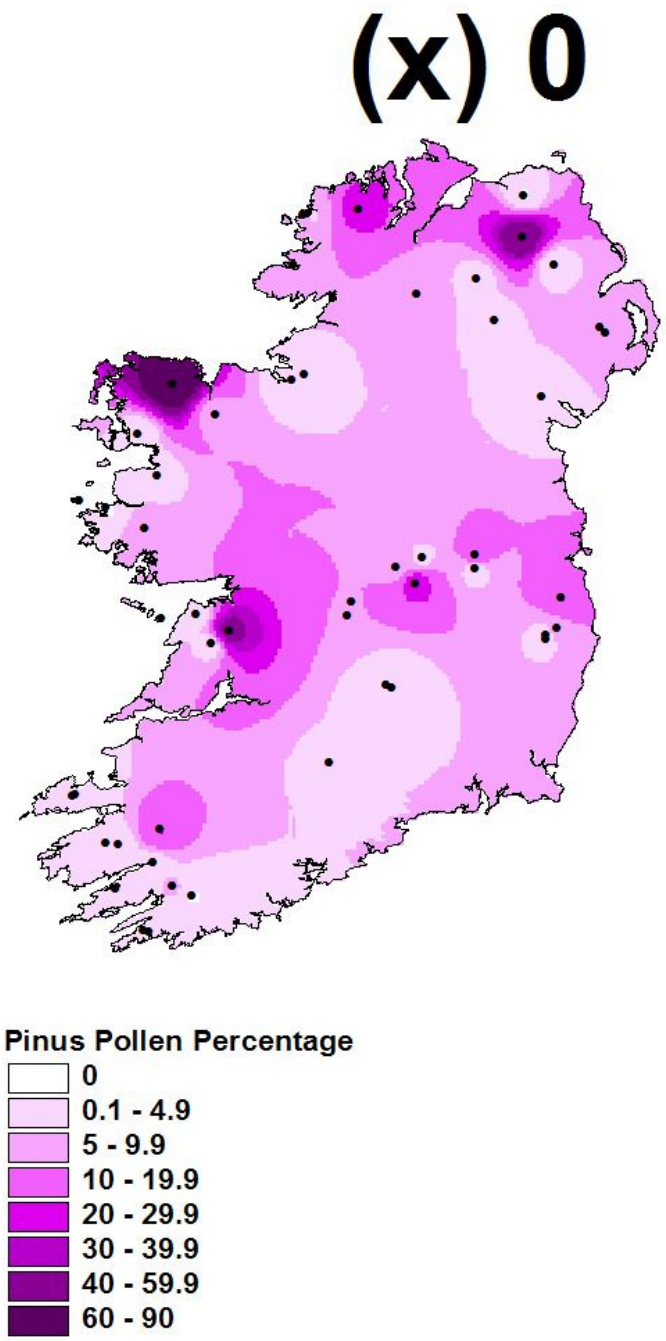
- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90

# (w) 500



**Pinus Pollen Percentage**

- 0
- 0.1 - 4.9
- 5 - 9.9
- 10 - 19.9
- 20 - 29.9
- 30 - 39.9
- 40 - 59.9
- 60 - 90


(x) 0
Pinus Pollen Percentage
0
0.1 - 4.9
5 - 9.9
10 - 19.9
20 - 29.9
30 - 39.9
40 - 59.9
60 - 90

*7000 – 2500 cal BP Decline (Fig. 2.3 j-t)*

The *Pinus* decline is particularly well illustrated by the isopoll maps (see slideshow in Appendix 2.1), which depict a progressive collapse of *Pinus* pollen frequencies throughout most of Ireland. A gradual decline began at 7000 cal BP (Fig. 2.2). This coherent spatial pattern moved from east to west. Climatic change, the expansion of blanket bog, competition with *Alnus glutinosa*, progressive soil deterioration, pathogens and human activity have all been cited as possible causes of this decline (Bennett, 1984). Accelerations in the rate of decline of the mean *Pinus* pollen frequency between 6500-6000 and again between 5000-3500 cal BP (Fig. 2.2) may represent the first and second *Pinus* declines.

The first *Pinus* decline was asynchronous and may have been caused by a combination of factors in different parts of Ireland. It has been attributed to climatic change (Bradshaw & Browne, 1987) and associated competitive interactions arising from the expansion of *Alnus* (Bennett, 1984), from 7500-5000 BP (8200-5700 cal BP) (Smith & Pilcher, 1973), and the spread of upland blanket peat (Bradshaw & Browne, 1987). Mitchell (1951) termed the intersection of falling *Pinus* values with rising *Alnus* values the "Boreal-Atlantic transition". The significant to highly significant positive correlations between *Pinus* pollen frequencies and altitude from 7000-6500 cal BP (Table 2.2) may represent the marginalisation of *Pinus* in lowland habitats. The replacement of *Pinus* by *Alnus* in river valleys, in response to increasingly waterlogged conditions, is not apparent on the isopoll maps however. This is probably due to the shortage of lowland valley sites in the dataset (Table 2.1) and the spatially and temporally intermittent establishment pattern of *Alnus* (Bennett, 1984). Reduced *Pinus* pollen frequencies occur during this period in upland areas too, such as the Nephin Begs, Wicklow and Galtee Mountains. At sites in the Nephin Begs and Wicklow Mountains, *Pinus* exhibited marked antagonistic relationships with the Ericaceae and *Sphagnum*, implicating the spread of blanket peat in the decline at these locations (Browne, 1986; Bradshaw & McGee, 1988). Highly significant negative

correlations between *Pinus* pollen frequencies and eastings from 6500 to 4500 cal BP (Table 2.2) are consistent with the view that *Pinus* was more abundant in the west of Ireland at this time. By 5500 cal BP (Fig. 2.3m), *Pinus* pollen frequencies had declined dramatically, even in the west and south-west where values had previously been especially high, and began to fall below 5% over large areas, with several sites registering null values. This indicates the extirpation of the species over large areas.

Despite being based on a total arboreal pollen sum, the previously published 5200 BP (Bradshaw, 2001) and 5000 BP (Bradshaw, 1993) isopoll maps of *Pinus* correspond well with their closest equivalents at 6000 and 5500 cal BP (Fig. 2.3 l, m). Although this correspondence is unsurprising as the maps are partly based on the same data, it does suggest that this methodology works well and that the maps for previously unpublished time intervals are also reasonable.

The second and final *Pinus* decline began around 5000-4000 cal BP (Smith & Pilcher, 1973). It was part of a wider pattern also recorded in England and northern Scotland (Gear & Huntley, 1991; Lageard *et al.*, 1999) and has been attributed to human activity and continued climatic change (Bradshaw & Browne, 1987). Preserved stumps provide unambiguous evidence that *Pinus* expanded on Irish bogs prior to its final decline. For example at about 4400 cal BP, it occurred on western lowland blanket bog at site 46 (Connemara National Park) (O'Connell *et al.*, 1988) (Plate 2.1) and midland raised bogs in Counties Offaly and Kildare, such as site 52 (Glashabaun) (McNally & Doyle, 1984) (Fig. 2.3p). It is thought that a climatic shift to drier conditions facilitated an invasion of the bog surface and a subsequent shift to wetter conditions caused increased waterlogging and renewed peat formation, resulting in the disappearance of *Pinus* through failure to produce viable seedlings (McNally, 1990). At 2500 cal BP, the mean *Pinus* pollen frequency reached its Holocene minimum (1.6%) (Fig. 2.2) and values of less than 5% suggest extirpation throughout Ireland, except in western Donegal, north Mayo and the Burren (Fig. 2.3s). Supporting evidence for the presence of *Pinus* was

provided by macrofossils in the Burren at site 63 (Gortlecka) at 2500 cal BP (Watts, 1984a) and stomata in western Donegal at site 4 (Altar Lough) until approximately 2360 cal BP (Fossitt, 1994).

*2000 – 500 cal BP Extirpation with possible localised exceptions (Figs. 2.3 t-w)*

During this period, the isopoll maps display *Pinus* frequencies below 5% through most of Ireland, except in some western outposts. Bradshaw and Browne (1987) cited the last recorded occurrences of *Pinus* as 1790±95 BP and 1620±130 BP from stumps in Killarney, County Kerry and Clonsast Bog, County Offaly respectively (McAulay & Watts, 1961; Watts, 1984a) and 1120±150 BP from pollen and macrofossils at Gortlecka (site 63) in the Burren (Watts, 1984a), although Watts expressed concern that this date might be too young. The isopoll maps clearly indicate local presence of *Pinus* in the Burren. In addition to the pollen and macrofossil evidence from Gortlecka, consistently high *Pinus* values ranging from 38-51% of total terrestrial pollen were recorded throughout this period, with a *Pinus* needle at about 1100 cal BP, at site 62 (Rockforest Lough) (Chapter 3). This is consistent with Watts' (1984a) 1120±150 BP date, suggesting that it is in fact correct. An undated pollen core from the Carron Depression, also in the Burren, exhibited low but persistent *Pinus* values throughout the uppermost part of the core (Crabtree, 1982). In south Connemara, about 40 km to the north-west, site 53 (Lough Namackanbeg) exhibited *Pinus* pollen frequencies of 8 to 12.5% throughout this period. It must be remembered, however, that the pollen frequencies for site 53 are based on an arboreal pollen sum (Table 2.1). A pollen frequency of 6% occurred at site 76 (Sheheree Bog) near Killarney at 1500 cal BP, although no stomata were recorded (Cooney, 1996). The isopoll maps also show discontinuous elevated pollen frequencies in Donegal, with sites 4 (Altar Lough) and 9 (Lough Mullaghlahan) exceeding 5% at 2000, 1000 and 500 cal BP, but the disappearance of stomata suggests that *Pinus* had already been extirpated at these sites (Fossitt, 1994). Isolated increases occurred in the north-east and south-west

at 500 cal BP, but due to their fleeting nature they are not thought to represent the local presence of *Pinus.*

Bradshaw and Browne (1987) attributed the final *Pinus* decline to human activity and increasingly waterlogged conditions on peatlands. As Watts (1984a) expressed some doubt over the 1120±150 BP date from Gortlecka, the specimen from Clonsast Bog, dated to 1,620±130 BP (McAulay & Watts, 1961), was previously thought to represent the last unequivocal record of indigenous *P. sylvestris*. The species was widely believed to have become extinct in Ireland at that point (White & Doyle, 1982; Webb *et al.*, 1996; Cross, 1998). Bradshaw and Browne (1987) concluded that *Pinus* populations must have been at biologically insignificant levels throughout the medieval period and that the extirpation or survival of the species could only be verified by finding datable remains in a natural setting. In light of recent research, included here as the data from Rockforest Lough, it appears that *Pinus* may have persisted in the Burren throughout the medieval period.

Although it remained well below the 5% threshold, the mean *Pinus* pollen percentage increased slightly from 1500-500 cal BP (Fig. 2.2). Again, this was partly due to high values at site 62. When site 62 was excluded from the calculation, the minimum mean frequency reached 1.2% at 2000 and 1500 cal BP, with increases observed thereafter. This increase is surprising, occurring as it does against the backdrop of the final *Pinus* decline through most of Ireland, as evidenced by the stomatal and pine stump records. The increase is not thought to represent the early reintroduction of *P. sylvestris* as the pattern is widespread and documentary evidence indicates that reintroduction did not occur until the late seventeenth or early eighteenth century (Pococke, 1891). This pattern may represent exaggeration of the long-distance component in an increasingly deforested Irish landscape.

*0 cal BP Reintroduction (Fig. 2.3x)*

The isopoll map from this most recent time interval shows dramatic change since 500 cal BP. It clearly reflects the introduction and reintroduction of *Pinus* species, as pollen frequencies exceed 5% over much of Ireland once more. *Pinus* pollen frequencies exceeding 40% signify the proximity of contemporary pinewoods to palynological sampling sites. For example, site 62 (Rockforest Lough) is located 500 m downwind from a *P. sylvestris* stand (Chapter 3) and site 27 (Croaghan East) amongst plantations of *P. contorta* (Dwyer, 1995). The presence of this apparently naturalised pinewood near Rockforest Lough and the continuously elevated *Pinus* pollen frequencies recorded from 2000-0 cal BP indicate that this may be an extant native population of *P. sylvestris*.

*P. sylvestris* of non-native origin had been introduced to Ireland by the eighteenth century. Pococke (1891) observed a thriving plantation of 20,000 "firres" near Coolnamuck, Carrick-on-Suir, County Tipperary in 1752. A documented reintroduction took place at Killarney, County Kerry around 1800 when *P. sylvestris* of Scottish provenance was planted extensively on the Kenmare and Herbert Estates (Radcliff, 1814; Watts, 1984b). This sequence of regional extinction and reintroduction of *P. sylvestris* is believed to have occurred in England, Wales, Denmark, Belgium and the Netherlands (Mirov, 1967; Jalas & Suominen, 1973; Bennett, 1984; Bradshaw, 1993; Le Maitre, 1998; Lust *et al.*, 2000). Both *P. sylvestris* and the North American *P. contorta* have been widely planted for forestry, particularly in the earlier twentieth century (O'Driscoll, 1980; Webb *et al.*, 1996), and *P. sylvestris* is naturalising in a variety of habitats (Kelly, 1981, 1985). The modern as well as the historic dynamics of the species in Ireland are therefore the subject of current research (Roche *et al.*, 2009, Chapter 4). There are some important distinctions to be made between modern Irish pinewoods and their ancient counterparts. A very low proportion (9.7%) of Ireland's land area is currently covered by forest and a very high proportion of this (86.5%) is comprised of plantations (FAO, 2007). In comparison with their former range, the modern pinewoods are now fragmented and limited in extent. This must be

considered when examining interpolated pollen frequencies (Fig. 2.3x). The majority of modern Irish pinewoods originated as plantations and many are managed for commercial forestry purposes, so they are relatively modified in nature. There is also the issue of infestation with the non-native *Rhododendron ponticum*, which is particularly pernicious in pinewoods in the south-west (Roche *et al.*, 2009). Finally, the biodiversity associated with Irish pinewoods has been impacted by the extirpation of faunal species such as the capercaillie (*Tetrao urogallus*) (van Wijngaarden-Bakker, 1985) and a suite of *Pinus*-dependent saproxylic invertebrates (Speight, 1985; Whitehouse, 2006; Reilly, 2008). The moss species *Ptilium crista-castrensis*, however, is one of the most characteristic species of Scottish pinewoods and was not known from Ireland until its discovery in a corrie on Mweelrea, County Mayo in 1987 (Blockeel, 1988; Kelly, 2005).

## 2.5. Conclusions

Spatial interpolation using GIS has been found to be an effective and objective method of isopoll mapping. This method could be used in the production of isopoll or isochrone maps for other taxa, locations or time periods. GIS was effective in generating hypotheses on the spatial and temporal distribution change of *Pinus* in Ireland, which could be further investigated by standard statistical approaches. Bennett's (1995) revised 5% critical pollen percentage was found to be useful and generally appropriate as a rough indication of the presence of *Pinus* around a palaeoecological sampling site. However, some departures from the 5% criterion were noted where low pollen frequencies coincided with other proxies indicating the local presence of *Pinus* (Fossitt, 1994; Cooney, 1996). This presents problems for palynological analysis of the colonisation and extirpation of *Pinus* and confirms Froyd's (2005) assertion that future research would benefit from the recording of stomata during routine pollen counting, thereby providing a better resolved account of the dynamics of *Pinus* at a given site.

The isopoll maps generally supported the patterns in the postglacial dynamics of *Pinus* in Ireland described by other authors. Although correlation does not necessarily imply causation, the results of correlation analysis were consistent with some of these patterns, such as the retreat of *Pinus* into upland areas during the period of *Alnus* expansion in Ireland and the east to west progression of the *Pinus* decline. However, the large dataset and multi-site perspective of the isopoll maps highlighted some new or previously poorly defined patterns. The accepted hypothesis of early postglacial colonisation by *Pinus* in south-west Ireland (Mitchell & Ryan, 1997) should be reviewed. The isopoll maps strongly suggest that *Pinus* arrived first in western Ireland and this is supported by macrofossil evidence from the Burren (Watts, 1984a). Stomatal analysis of early postglacial sequences from the south-west would be informative here. Another difference is the high pollen values observed in the Burren, centred on the recently analysed site 62 (Rockforest Lough) from 2000-0 cal BP, when *Pinus* supposedly became extinct in Ireland. This pattern may represent the persistence of an extant native population of *P. sylvestris* and is the subject of current research (Chapter 3).

One practical application of these isopoll maps is in woodland restoration. Ireland's native woodlands are relatively scarce and highly fragmented (Perrin *et al.*, 2006; Perrin *et al.*, 2008b). The Native Woodland Scheme provides grant aid to landowners for the planting of native trees (Forest Service, 2001). Despite its disputed native status as a reintroduced species, *P. sylvestris* has been included in this scheme and is being widely planted in semi-natural habitats. The isopoll maps, showing the former range of *P. sylvestris* in Ireland, could be used to inform site selection for new plantings of *P. sylvestris* and species selection at any given site. The database of dated, regional postglacial pollen sequences presented here may be used as a basis for meta-analyses of other taxa, while the isopoll maps may contribute to future research on the postglacial dynamics of *Pinus* in Ireland.

# 3. Palaeoecological evidence for the continued survival of Scots pine (*Pinus sylvestris*) through the late Holocene in the Burren, western Ireland

To be submitted as: Jenni R. Roche, S. Waldren, B. Stefanini and F.J.G. Mitchell. Palaeoecological evidence for the continued survival of Scots pine (*Pinus sylvestris*) in the Burren, western Ireland. *Biological Conservation.*

Plate 3.1. Photograph of the pinewood at Rockforest with Mullaghmore in the background, taken on April 13th 2006.

## 3.1 Abstract

The decline and presumed extinction of *Pinus* in Ireland is of great interest as its date varies considerably and the presumed cause differs among sites. The available evidence suggests that *Pinus* survived until relatively late in the Burren, western Ireland. This study aimed to examine the vegetation history of an apparently naturalised pinewood at Rockforest in the Burren National Park, with particular reference to the *Pinus* decline. Pollen, macrofossil and loss on ignition data from Rockforest Lough covering the last 2000 years are presented and interpreted in relation to historical sources. A relatively stable vegetation history was recorded, despite considerable human activity. The dominant vegetation type was an open pinewood with abundant *Corylus*. Woodland cover seems to have been continuous, although a gradual expansion of open ground, particularly grassland, was recorded. This may be attributable to the management of the Rockforest Estate. Remarkably, a *Pinus* decline was not recorded. Macrofossils demonstrate the local presence of *Pinus* at 1110 ± 60 cal BP (AD 840) and *Pinus* pollen is represented continuously from 2000 cal BP (50 BC) to the present day at values consistently in excess of 38%. This indicates that a relict population of *P. sylvestris* persisted in the Burren to the present day, the pinewood at Rockforest being the most likely candidate. This research strongly suggests that the widely accepted hypothesis that *Pinus* became extinct in Ireland is incorrect. These findings have wide-ranging and significant implications for palaeoecological research and the conservation management of *P. sylvestris* in Ireland.

## 3.2 Introduction

### 3.2.1 Postglacial History of *Pinus* in Ireland

*Pinus sylvestris* L. (Scots pine) was once indigenous and widespread throughout north-west Europe. Extensive *Pinus* forests occurred in the northern European lowlands as the Holocene opened but had begun to decline by about 8900 cal BP (6950 BC). By about 5700 cal BP (3800 BC), the species remained dominant only in the northern boreal forests, sparsely on dry soils in the central European lowlands and in small isolated pockets in the northern European lowlands, Britain and Ireland (Huntley & Birks, 1983). The species is believed to have been extirpated and subsequently reintroduced in several north-west European countries, namely Belgium, the Netherlands, Denmark, England, Wales and Ireland (Mirov, 1967; Jalas & Suominen, 1973; Bennett, 1984; Bradshaw, 1993; Le Maitre, 1998; Lust *et al.*, 2000).

*P. sylvestris* colonised Ireland relatively early in the Holocene (Chapter 2), with one of its earliest occurrences being recorded at Gortlecka in the Burren at about 10,500 cal BP (8550 BC) (Watts, 1984a). *P. sylvestris* forms stable vegetation communities on nutrient-deficient soils, indicating a high competitive ability under these conditions. However, it cannot tolerate heavy shade from other trees (Carlisle & Brown, 1968) and its distribution is heavily influenced by competitive interactions. In Ireland, *Pinus* was probably largely restricted to areas unsuited to its main competitors, *Ulmus* and *Quercus*, which favoured lowland central and eastern soils of high base status. *Pinus* was the dominant arboreal pollen type in almost all western and most upland study sites for at least part of the early postglacial and formed an important component of certain marginal habitats, such as raised bogs, river valleys and uplands (Bennett, 1984; Bradshaw & Browne, 1987; Chapter 2). It occurred mainly in areas of acidic peat or siliceous bedrock, but also on the limestone pavement of the Burren (Watts, 1984a), where patchy, shallow soils exhibit periodic drought and low levels of available nitrogen and phosphorus. These conditions are unsuitable for most deciduous tree species but *Pinus* tolerates them, lending it a competitive advantage in such habitats (Bennett, 1984).

The mid-Holocene *Pinus* decline is recognised as an important pollen stratigraphic event. It occurred in Ireland around 4500 cal BP (2550 BC) (Smith & Pilcher, 1973; Chapter 2) and has also been recorded in England (Lageard *et al.*, 1999) and northern Scotland (Gear & Huntley, 1991). This event has been attributed to human activity and climatic change (Bradshaw & Browne, 1987). In Ireland, late outposts of *Pinus* are known to have occurred at three western sites and one midland raised bog. The pollen signal from a *Pinus* population at Slish Wood, County Sligo disappeared at 1810 ± 260 cal BP (AD 140) (Dodson & Bradshaw, 1987). Pine stumps from the Killarney valley were dated to 1740 ± 110 cal BP (AD 210) and 1720 ± 110 cal BP (AD 230) (Watts, 1984a). *Pinus* pollen and macrofossils from Gortlecka in the Burren were dated to 1050 ± 160 cal BP (AD 900) (Watts, 1984a), although the author expressed concern that this date may be too young. The most recent unequivocal record came from a preserved pine stump from Clonsast Bog in County Offaly, which was dated to 1550 ± 140 cal BP (AD 410) (McAulay & Watts, 1961). *P. sylvestris* is widely believed to have become extinct in Ireland at this point, during the early medieval period (Webb *et al.*, 1996). The supposed extirpation of *Pinus* in Ireland is of great interest as the date varies considerably between regions and the apparent causal factors differ between sites (Watts, 1984a). Bradshaw and Browne (1987) called for careful palaeoecological work to investigate whether contemporary *Pinus* populations originated from relict individuals, concluding that whether the species became totally extinct or not could only be determined by finding datable remains in a natural setting. The question of whether any relict populations of *P. sylvestris* persisted in Ireland remains open at present.

An apparently naturalised pinewood occurs on limestone pavement in the townland of Rockforest (also known as Magheranraheen), within the Burren National Park. Mature but stunted Scots pines form scattered standards among patches of *Corylus*-dominated scrub (Plate 3.1). *P. sylvestris* is regenerating, with a range of age classes represented. The woodland is species-rich and semi-natural in character and its vegetation is described in more detail by Roche *et al.* (2009).

Similar open stands of apparently naturalised *P. sylvestris* on limestone pavement are known from Rockvale, also in the east Burren, Coole Park and Castletaylor in County Galway and Ballykine and Keel Bridge in County Mayo.

This study aims to investigate the vegetation history of Rockforest and the wider Burren area over the last 2000 years, with particular reference to the dynamics of *Pinus*. Palaeoecological methods are the most effective in determining if a woodland has a long history (Mitchell, 1988), but present-day observations and archaeological and historical data sources are also considered in the interpretation of the palaeoecological data.

### 3.2.2 Aspects of the Local History of Rockforest

It is essential to use available archaeological and historical sources in the interpretation of palynological data from the late Holocene. When linked with historical records of human activity and population density, observed fluctuations in arboreal and non-arboreal pollen may be interpreted as periods of deforestation or forest regeneration (van Geel & Middeldorp, 1988).

The old Irish name for the townland of Rockforest was *Machaire an Ráithín*, which means the plain of the little fort (http://www.logainm.ie/ 4/12/2008). A long history of human activity is evident from the range of archaeological monuments of different periods in the surrounding area. These include megalithic tombs, ringforts, *fulachtaí fia* (putative cooking pits), churches and castles. Humans have probably occupied the Burren intensively for at least the last 2500 years (Watts, 1984a), covering the duration of this study. Specific references to the townland in the historic literature attest to the continuity of its woodland cover and to continued human activity. In the fourteenth century, the area was known as *Coill ó Flanchadha* (the wood of O'Flanchada) (Frost, 1893). The pass of *Bealach an Fhiodhfail*, then the principal route from Galway to Clare and now

from Gort to Corofin, ran through *Coill ó Flanchadha* and directly through Rockforest townland. A battle took place there in AD 1311 (MacCraith, 1929) and an army marched through in 1599, sending raiding parties into the surrounding countryside (O'Donovan, 1851). A remnant of Sir Donat's Road, probably dating from the late seventeenth or early eighteenth century, also runs through the townland.

Henry Pelham's Grand Jury Map of County Clare (1787) shows woodland cover at Rockforest but relatively little in the surrounding area. Rockforest House, located beside Rockforest Lough, was built by the Blood family in the late eighteenth century. Their estate included a finely planted demesne extending nearly a mile along the road, with a walled garden, ice house and grain silo (Lewis, 1837; Weir, 1999). By 1808, Bindon Blood had planted over 80 acres of light, rocky soil of low agricultural value with *Larix*, *Fraxinus*, *Quercus*, *Ulmus*, *Fagus*, *Betula*, *Picea*, *Alnus*, *Acer*, *Pinus sylvestris*, *P. pinaster* and other species (Dutton, 1808). The first edition of the Ordnance Survey six inch maps (1840) depicts an estate dominated by "fir plantations" (*P. sylvestris* was commonly known as fir at this time) interspersed with rocky, heathy pasture, parkland, fields, field boundaries, orchard, brushwood, lakes, areas liable to flood, buildings and tracks. The second edition (1899) shows a similar mosaic but with a shift from fir plantation to mixed woodland. This shift must be interpreted with caution however, due to differences in the map legend's classification of vegetation features between the two editions (P. Ferguson, pers. comm.). In the twentieth century, some woodland clearance was carried out for agricultural purposes and taller, straight specimens of *P. sylvestris* were selectively felled (J. Cunningham, pers. comm.). The timber grown at Rockforest was locally regarded as being of the highest quality (Brew, 1998). As shown in Plate 3.2, Rockforest Estate still consists of a mixture of agricultural land, woodland and scrubby rock (Weir, 1999).

### 3.2.3 Coring Site Description

Rockforest Lough (Irish Grid Reference R 356 953; 08° 57'W, 53° 00'N) is located 10 km north-east of Corofin, Co. Clare, in western Ireland (Fig. 3.1). It lies on Carboniferous limestone at an altitude of 16 m above sea level. The site lies within the Burren, a karstic limestone region, extending over 300 $km^2$, well known for its botanical diversity and rich archaeological heritage. The area exhibits a mild, moist oceanic climate. Precipitation is high with a mean annual rainfall of 1582 mm being recorded (1951-1980) at Inagh, Co. Clare, about 20 km to the south-west. The mean daily temperature for the warmest month, August, is 15.7° C and the coldest month, January, is 5.0° C (Rohan, 1986). The lake is approximately 700 m in length and features a deep basin (7.48 m) with a shallower arm extending to the north-east. The total area of the lake is approximately 0.08 $km^2$. The water level of the basin is relatively stable (J. Cunningham, pers. comm.). The lake is fringed by reeds with flat, open limestone pavement to the north and a strip of glacial till supporting pastoral farmland to the south. Rockforest House is situated adjacent to Rockforest Lough and the pinewood is located about 500 m south-west of the lake (Plate 3.2).


Figure 3.1. Location map of Rockforest Lough and selected surrounding palaeoecological sampling sites.


Plate 3.2. Aerial photograph taken in 2000, showing (1) the pinewood at Rockforest, (2) part of Rockforest Lough, (3) Rockforest House and the surrounding landscape.
Scale: approximately 3 km x 2.5 km.
Source: National Inventory of Architectural Heritage, www.buildingsofireland.ie/cgibin/displayimage.cgi?id=3536&size=f&type=a1, Accessed 12/10/2009.

## 3.3 Methods

### 3.3.1 Site Selection

Small, wet hollow sampling sites permit the reconstruction of woodland history at the local scale (Mitchell, 1988), but no suitable deposits were found within the

woodland at Rockforest. Watts (1984a) describes the difficulties associated with obtaining satisfactory palaeoecological sampling sites in the karstic limestone of the Burren. Turloughs are subject to hiatuses and redeposition, while *Cladium mariscus* swamps display poor pollen preservation and lakes containing carbonate mud can be unsuitable for radiocarbon dating due to the hard water effect. Permanent lakes containing brown algal mud are preferable for sampling as pollen preservation is better and the hard water effect less pronounced. However, lakes recruit pollen from relatively large areas, recording vegetation dynamics at the regional scale. Rockforest Lough was selected for sampling as it was the closest suitable site to the woodland under investigation. As a small to medium sized lake (0.08 $km^2$), the relevant pollen source area of the site was expected to cover 300-800 m (Sugita, 1994). This site was therefore expected to provide a predominantly extralocal pollen record (Jacobson & Bradshaw, 1981), which would be an appropriate pollen source area for the purposes of this study.

### 3.3.2 Coring

Coring was carried out on the 18$^{th}$ and 19$^{th}$ of June 2008. The coring location was in the deep basin (7.48 m), the deepest part of the lake. A short core (RFB, 81 cm) was taken using a rod operated modified plexiglass piston corer, retaining the undisturbed sediment/water interface. This core was extruded vertically at 1 cm intervals in the field. Overlapping cores of the lower sediments (RFC) were extracted with a Livingstone corer (Livingstone, 1955) driven through casing to 552 cm depth. The core sections were wrapped in the field, stored at 4$^{o}$C and sliced at 1 cm intervals in the laboratory.

### 3.3.3 Pollen Analysis

Pollen analysis was carried out on 1 cm thick samples at 8 cm intervals, decreasing to 4 cm in the uppermost part of the core. Subsamples of 0.5 $cm^3$ of sediment

were prepared according to standard procedures of potassium hydroxide digestion, hydrochloric acid treatment, hydrofluoric acid treatment and acetolysis (Moore *et al.*, 1991). *Lycopodium* tablets were added to allow the calculation of pollen concentrations (Stockmarr, 1971). Samples were mounted in silicone oil and counted using an Olympus BX40 microscope at x400 magnification and under oil immersion at x1000 where necessary. Pollen and spores were identified using the key and illustrations of Moore *et al.* (1991), the illustrations of Reille (1992) and Beug (2004) and reference material held by the Department of Botany, Trinity College, Dublin. Nomenclature followed Moore *et al.* (1991), except for the Coryloid, Urticaceae, *Polypodium* and *Rumex* taxa, where species have been amalgamated. Coryloid pollen was assumed to be predominantly *Corylus*, which is far more abundant than *Myrica gale* in the Burren (Webb & Scannell, 1983). A minimum of 400 identifiable terrestrial pollen and spores were counted from each sample. The slides were also examined for *Pinus* stomata. The pollen counts were expressed in a percentage pollen diagram using TILIA 2.0.b.4 (Grimm, 1991). The pollen sum calculation was total terrestrial pollen and spores, including indeterminate grains and excluding the aquatic taxa *Apium inundatum* type, *Caltha* type, *Hydrocharis morsus-ranae*, *Lemna*, *Myriophyllum alterniflorum*, *Nymphaea alba* type and *Nuphar*. The proportion of indeterminate grains was rather high due to poor pollen preservation. Due to its distinctive pollen morphology, *Pinus* was unlikely to be counted as indeterminate. Consequently, it was decided to include indeterminate grains in the pollen sum to prevent overestimation of the relative abundance of *Pinus.* Concentration values were checked to confirm that no major pollen changes occurred which were not apparent in the percentage pollen diagram.

### 3.3.4 Loss on Ignition

To ensure a sufficient amount of material for analysis, loss on ignition was carried out on 2 cm thick samples. Oven-dried, weighed samples were heated in a furnace

for 30 minutes at 150° C, one hour at 180° C, 30 minutes at 200°, 220° and 240° C, one hour at 300° C and five hours at 550° C to estimate organic content and for a further three hours at 950° C to estimate carbonate content by percentage loss on ignition analysis. The loss on ignition profiles were used to match the overlapping cores (Appendix 3.1). Mean values were then calculated for the overlapping portions, so that organic matter and carbonate content could each be graphed as a single curve. The percentage organic and carbonate content values were summed and subtracted from 100, giving the percentage of in-washed mineral material (Lamb & Thompson, 2005).

### 3.3.5 Spheroidal Carbonaceous Particles

The extraction of Spheroidal Carbonaceous Particles (SCPs) followed Rose (1990, 1994) with some modifications due to low numbers of SCPs and an abundance of fine material in the sediment. Sample dry weights were increased to between 0.6 and 4.7 g and volumes of solvents were increased accordingly. After extraction, samples were filtered through a 10 μm sieve to remove the fine material and facilitate counting. This may also have removed smaller SCPs from the residue, with selective removal of SCPs from oil combustion, as these are generally smaller than SCPs from coal combustion (Rose, 1990).

### 3.3.6 Radiocarbon Dating

To avoid problems associated with the hard water effect, terrestrial plant macrofossils were hand-picked or sieved from the sediments (Andrée *et al.*, 1986; Cwynar & Watts, 1989). Nine such samples were radiocarbon dated using accelerator mass spectrometry (AMS) analysis. Radiocarbon ages were calibrated using CalPal-2007 Online (Danzeglocke *et al.*, 2009). A chronology was generated by linear interpolation between the top of the core and the SCP and AMS dates, excluding inverted dates.

## 3.4 Results

### 3.4.1 Sediment Stratigraphy

The sediment stratigraphy consisted of homogeneous brown algal mud throughout the uppermost 111 cm described in this study. Macrofossils were scarce, as demonstrated by the need to sieve samples to obtain sufficient material for radiocarbon dating. A *Pinus* needle was recovered at 66 cm and a *Pinus* wood fragment at 153 cm. Although the pollen analysis slides were examined for *Pinus* stomata, none were recorded.

### 3.4.2 Loss on Ignition

The loss on ignition profiles of the overlapping portions of the RFB and RFC cores exhibited similar patterns, allowing the cores to be matched satisfactorily (Appendix 1). While pollen analysis was conducted to 111 cm depth (2000 cal BP, 50 BC), loss on ignition analysis was conducted to 152 cm depth (5730 cal BP, 3780 BC), providing a relatively long record. The mineral content profile was characterised by periods of stability with occasional systematic shifts to higher or lower values (Fig. 3.2). The overall mean was 32.5%. Mineral input remained relatively static from 152-98 cm (5730-1390 cal BP, 3780 BC-AD 560), with values averaging 33.8%. A local minimum (26.3%) occurred at 94 cm (1360 cal BP, AD 590). Mineral content decreased somewhat from 92-56 cm (1340-960 cal BP, AD 610-990), averaging 31.7%. A local maximum of 37.1% was reached at 54 cm (930 cal BP, AD 1020). This was followed by a systematic shift to relatively low values from 46-36 cm (810-670 cal BP, AD 1140-1280), averaging 27.5%. The overall minimum (21.2%) occurred at 34 cm (640 cal BP, AD 1310). This was followed by two systematic shifts to higher values, averaging 33.9% from 32-12 (610-100 cal BP, AD 1340-1850) cm and exceeding 38% from 10-6

cm (60-20 cal BP, AD 1890-1930), the highest values of the profile. A period of instability occurred from this point to the present day.

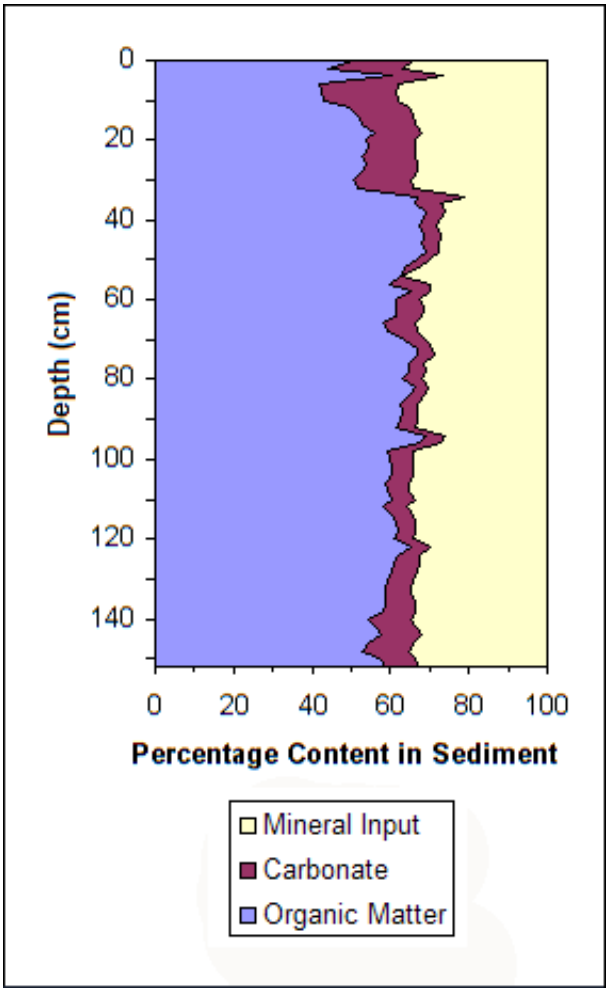



Figure 3.2. Organic matter and carbonate content loss on ignition profiles for Rockforest Lough.

### 3.4.3 Chronology

The SCP concentration profile (Fig. 3.3) shows that the start of the SCP record occurred at 12 cm, dating this level to AD 1850 ± 25 (Rose & Appleby, 2005) (Table 3.1). Variation in the profile prevented the objective identification of the

1950s/1960s rapid increase. The subsurface peak was not apparent but this feature is not always present in Irish cores (Rose *et al.*, 1995).

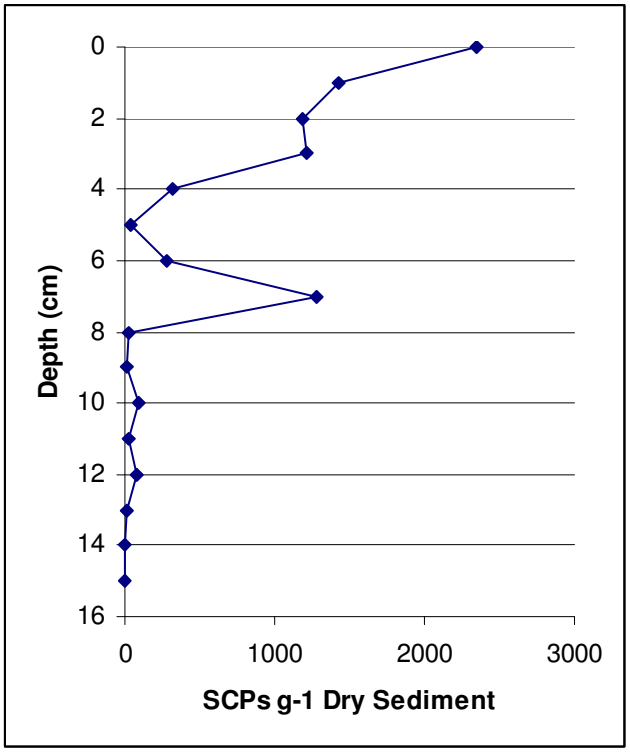



Figure 3.3. Spheroidal Carbonaceous Particle concentration profile for Rockforest Lough.

Nine AMS dates were obtained from terrestrial plant macrofossils (Table 3.1). Two of these were inverted. The date at 22 cm was only slightly younger than expected and remained largely within the standard deviation of the adjacent date at 19 cm. The date at 72-74 cm appeared much too old relative to others in the dataset. It was decided to exclude the inverted dates from the age-depth model.

The age-depth model was based on the top of the core, one SCP date and seven AMS dates (Fig. 3.4). The curve for the period in question is relatively smooth and the chronologies of the RFB and RFC cores matched well. The sediment accumulation rate was relatively constant from 1400 cal BP (AD 550) to the present day (0.7 mm $yr^{-1}$) but was considerably slower before this time (0.1 mm $yr^{-}$

[1]). The time span covered here should ensure that the pollen record opens before the presumed extirpation of *Pinus* in the Burren at 1050 ± 160 cal BP (900 AD) (Watts, 1984a).

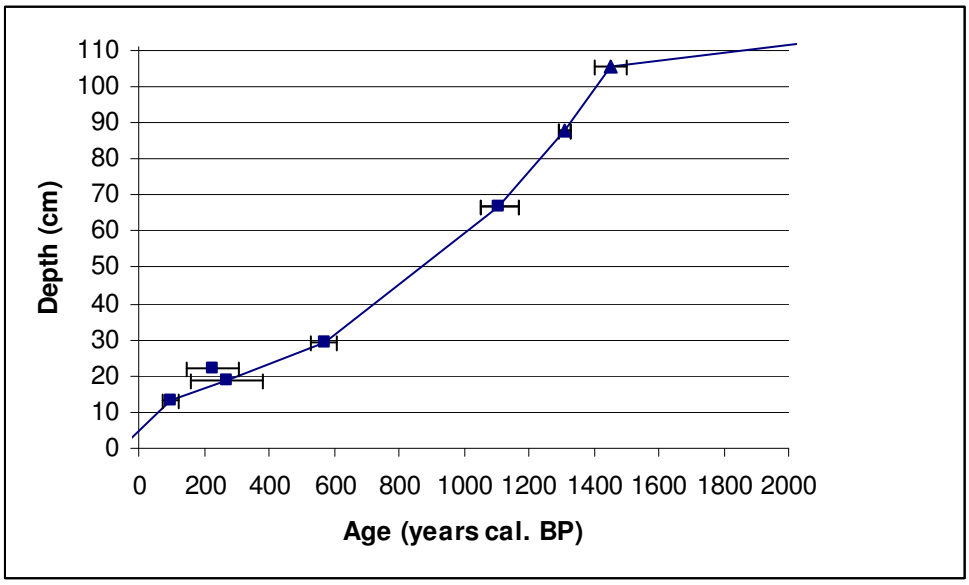



Figure 3.4. Age-depth model for Rockforest Lough (0-2000 cal BP). Dates from the RFB core are denotes by squares, the RFC core by triangles.

Table 3.1. Accelerator Mass Spectrometer and Spheroidal Carbonaceous Particle dates from Rockforest Lough cores RFB and RFC.

| Core | Depth (cm) | Laboratory reference | Sample description | Uncalibrated age (years BP) | Calibrated age (cal. years BP) | Calendric age (cal. AD/BC) |
|---|---|---|---|---|---|---|
| RFB | 12 | - | Start of SCP record | - | 100 ± 25 | AD 1850 ± 25 |
| RFB | 19 | Beta – 247933 | Wood | 240 ± 40 | 270 ± 110 | AD 1680 ± 110 |
| RFB | 22 | Beta – 247934 | Plant material | 230 ± 40* | 230 ± 80 | AD 1720 ± 80 |
| RFB | 29 | Beta – 247935 | Wood | 520 ± 40 | 570 ± 40 | AD 1380 ± 40 |
| RFB | 66-68 | Beta – 252787 | Plant material | 1180 ± 40 | 1110 ± 60 | AD 840 ± 60 |
| RFC | 72-74 | Beta – 252788 | Organic material | 3410 ± 50* | 3670 ± 70 | 1720 ± 70 BC |
| RFC | 88 | Beta – 253480 | Plant material | 1380 ± 40 | 1310 ± 20 | AD 640 ± 20 |
| RFC | 104-107 | Beta – 252790 | Plant material | 1540 ± 40 | 1450 ± 50 | AD 500 ± 50 |
| RFC | 153 | Beta – 252791 | *Pinus* wood | 5050 ± 40 | 5810 ± 60 | 3860 ± 60 BC |
| RFC | 495 | Beta – 247936 | Nutshell | 8860 ± 60 | 9970 ± 140 | 8020 ± 140 BC |

Dates were calibrated using CalPal-2007 Online (Danzeglocke *et al.*, 2009) and are quoted with a standard deviation of 2σ (95% confidence limit).
* Inverted dates

### 3.4.4 Pollen Stratigraphy (111-0 cm, 2000 cal BP - present)

In total, 68 terrestrial taxa were recorded. A percentage pollen diagram of selected taxa is presented in Figure 3.5. The profile shows relatively small fluctuations in the frequencies of individual taxa rather than dramatic changes in the overall vegetation. It is dominated by arboreal pollen throughout, ranging from a minimum of 54.6% to a maximum of 73.0%. The most obvious feature is the continuously high level of *Pinus*. *Pinus* frequencies are highest at the base of the profile (51.3%). They fluctuate somewhat over time but at no point do they drop below 38.2%. *Corylus* is a significant component of the pollen sum throughout, with *Betula*, *Alnus*, *Quercus* and *Ulmus* present at low values. Where peaks in *Fraxinus* frequencies occur, they coincide with peaks in *Ulmus.* *Fagus* appears in the upper half of the profile. Gramineae dominate the non-arboreal component, exhibiting a gradual increase over time, from 3.5% at the base to 10.3% at the top of the profile. Cerealia and *Pteridium aquilinum* are represented almost continuously at low levels. *Plantago lanceolata*, *Calluna vulgaris*, Cyperaceae, Lactuceae, Caryophyllaceae and *Polypodium* are also present at lower values throughout.

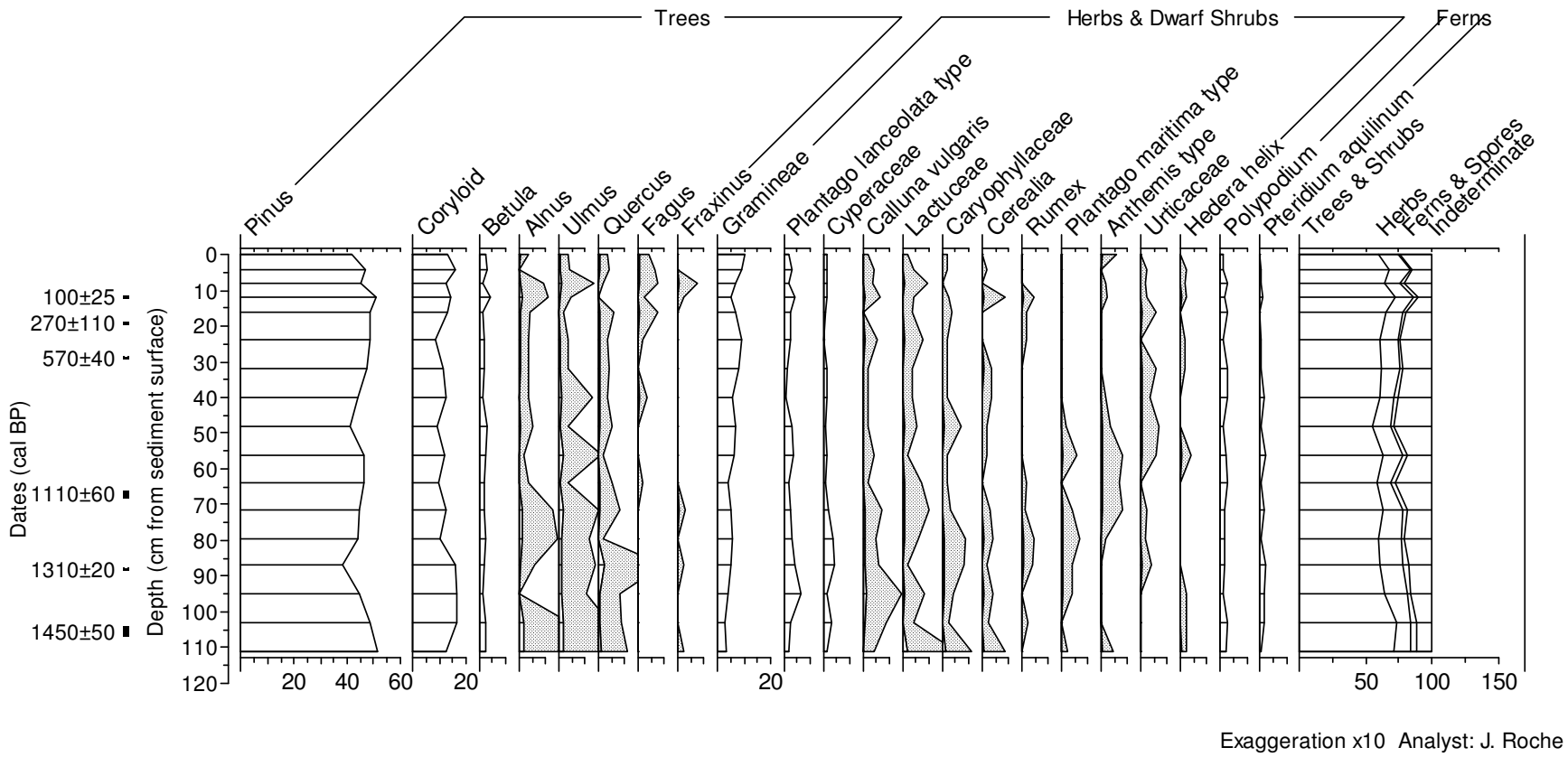



Figure 3.5. Percentage pollen diagram of selected taxa from Rockforest Lough.

## 3.5 Discussion

### 3.5.1 Landscape and Woodland Structure

The pollen record indicates a relatively stable vegetation history over the last two millennia, although it does record some changes in woodland cover and land use (Fig. 3.5). The consistently high level of arboreal pollen indicates that the area has supported woodland continuously over the last two millennia. This corresponds with the map evidence and historic literature available from the fourteenth century onwards. The relatively high values of *Pinus* and *Corylus* suggest that these were the dominant tree species, while *Betula* and, to a lesser extent, *Quercus* and *Ulmus* were present at lower frequencies. The *Alnus* signal may represent regional pollen as it never appeared in the macrofossil record at Gortlecka (Watts, 1984a) and is rare in the Burren today (Webb & Scannell, 1983). The dominance of *Pinus*, a light-demanding species (Carlisle & Brown, 1968), points to an open woodland structure. The *Calluna* curve suggests that heathy vegetation was present as an understorey in these open pinewoods and/or in open situations. Indeed, the significant proportion of non-arboreal pollen, including light-demanding taxa such as *Plantago lanceolata* and *Pteridium aquilinum*, indicates that the tree canopy was absent in at least part of the woodland (Behre, 1981). The landscape was therefore likely to consist of a mosaic of different habitats. The frequency of Gramineae and *Plantago lanceolata* suggests that the landscape included areas of open grassland. The large number of taxa recorded is consistent with the pattern of a diverse habitat mosaic.

### 3.5.2 Vegetation Dynamics and Human Activity

Human activity was evident throughout the study period from reductions in woodland cover and the presence of indicator taxa, which are discussed in detail below. This is consistent with the archaeological and documentary evidence outlined previously.

Relatively high levels of arboreal pollen (71%) occurred at the base of the profile, from around 2000-1450 cal BP (50 BC-AD 500). Light-demanding herbs and dwarf shrubs, such as Gramineae, *Plantago lanceolata*, *Pteridium aquilinum* and *Calluna vulgaris* were poorly represented at this time. This period may correspond to the Late Iron Age Lull, when a substantial reduction in farming activity is thought to have resulted in widespread regeneration of woody vegetation. This distinctive feature is recorded in several Irish pollen diagrams from about 1950-1450 cal BP (AD 1-500) (Mitchell, 1965; Molloy & O'Connell, 1993; Weir, 1995; Molloy & O'Connell, 2004; Molloy, 2005; Newman *et al.*, 2007) including Molly's Lough (Lamb & Thompson, 2005) and Lios Lairthín Mór (Jeličić & O'Connell, 1992), which are located relatively close to Rockforest Lough (Fig 3.1).

In the subsequent early medieval period, from about 1450-1300 cal BP (AD 500-650), arboreal pollen values declined while non-arboreal pollen values increased, suggesting increased farming activity. The peaks in *Calluna* and *Pteridium aquilinum* indicate reduced woodland cover while increases in Gramineae and *Plantago lanceolata* indicate pastoral farming. This pattern is also observed in several Irish pollen diagrams at this time (Weir, 1995; Lamb & Thompson, 2005; Molloy, 2005; Newman *et al.*, 2007).

Mixed farming seems to have been practised in the area throughout the study period. The representation of Gramineae increased fairly steadily from the early medieval period (1450 cal BP, AD 500) to the present day, indicating the opening up of the woodlands and the expansion of grassland over time. Cerealia are also

represented almost continuously throughout the profile, albeit at low levels, demonstrating human activity and the cultivation of arable crops in the area.

Aside from the aforementioned gradual rise in Gramineae, there appears to have been little net change in the vegetation during the rest of the early medieval period. The mineral content profile remains relatively stable until 940 cal BP (AD 1010), when a peak in mineral input is recorded at 54 cm (Fig. 3.3). This may indicate increased human activity within the lake catchment but if so, this is not manifested in the pollen evidence.

A gradual increase in the proportion of arboreal pollen was recorded from the beginning of the medieval period until the mid-nineteenth century (850-100 cal BP, AD 1100-1850). This partly coincides with a systematic shift to relatively low levels of mineral input from 810-670 cal BP (AD 1140-1280), possibly indicating a slackening of human activity in the area. Conversely, a systematic shift to increased levels of mineral input occured from 610-110 cal BP (AD 1340-1840) and may represent significantly increased human activity. Its initiation coincides closely with the first reference to the pass of *Bealach an Fhiodhfail* in 1311 AD (MacCraith, 1929) but it did not register in the pollen record. This episode of increased mineral input also coincides with the construction of Rockforest House, adjacent to the lake, during the late eighteenth century and the plantation and development of the estate (Dutton, 1808; Lewis, 1837; Weir, 1999).

The consistently elevated arboreal pollen values during this period contrast with the reduced values recorded from other Irish pollen diagrams, from the Burren and elsewhere, at this time. The population of Ireland reached almost 9 million prior to the Great Famine of 1845, resulting in unprecedented land use pressure. In many areas, poorer land was being cleared and converted to farmland to meet the needs of the growing population (Cole & Mitchell, 2003). In a pollen diagram from Cappanawalla in the Burren, for example, Feeser & O'Connell (2009) recorded arboreal pollen values of just 4% during the period 250-100 cal BP (AD

1700-1850). Indeed, Foot (1864) reported that wood was so scarce in the Burren that *Pteridium aquilinum* and *Dryas octopetala* were collected for firewood. This inconsistency between the pollen profiles from Rockforest Lough and other locations may be related to the management of the Rockforest Estate and the local dynamics of *Pinus*, which are discussed in detail below. The plantation of at least 80 acres of the Rockforest Estate (Dutton, 1808) is borne out by sustained high values of arboreal pollen and the appearance of the rational limit, i.e. the point at which the pollen curve begins to rise to sustained high values (Smith & Pilcher, 1973), of the non-native *Fagus* (Webb *et al.*, 1996) at the turn of the twentieth century. By that time, Ireland's landscape was almost treeless except for woodland remnants that had survived within the old estates (Hickie, 2002) and it appears that Rockforest was one such estate.

The period from 100 cal BP (AD 1850) to the present day is one of relative instability and, apparently, intensive human activity. Although it fluctuated somewhat, the proportion of arboreal pollen exhibited an overall decrease. The *Corylus* signal bucked this general trend by exhibiting an overall increase throughout this period, while a brief and isolated peak in *Fraxinus* at 50 cal BP (AD 1900) coincides with a peak in *Ulmus* values. This pattern is familiar. In a review of Irish pollen diagrams, Mitchell (1956) noted that the pollen values of *Fraxinus* and *Ulmus* often peak and decline simultaneously while *Corylus* shows a corresponding increase. In this case, the increase in the abundance of *Corylus* relative to *Pinus* and *Betula* indicates increased intensity of woodland clearance. *Corylus* regenerates more readily than other tree species in response to cutting and browsing (Lamb & Thompson, 2005). Original woodland has been known to degenerate into *Corylus* scrub as a result of continued human interference and *Fraxinus* may expand in response to the opening up of artificial clearances (Mitchell, 1956). Watts (1984a) concluded that the pattern of simultaneous contraction and expansion of *Fraxinus* and *Ulmus* is not replicated in the Burren but the pollen profile from Rockforest Lough contradicts this. The peaks in *Fraxinus* and *Ulmus* also coincide with peak values of *Fagus*. All three taxa were

included in the planting of the Rockforest Estate (Dutton, 1808), so the maturation of the plantation probably contributed to their representation at 50 cal BP (AD 1900). Increases were observed in the representation of *Plantago lanceolata* and *Pteridium aquilinum* during this period, while Gramineae reached maximum values at the top of the core. These patterns indicate the continued expansion of open ground, particularly grassland. Indeed, the strip of glacial till to the south of Rockforest Lough currently supports pastoral farmland (Plate 3.2). Mineral input reached a maximum around 50 BP (AD 1900), indicating intensive human activity in the lake catchment. All of these proxies are consistent with the tree felling and scrub clearance that are known to have been carried out on the Rockforest Estate during the twentieth century (J. Cunningham, pers. comm.).

### 3.5.3 Pollen Source Area

As a small to medium sized lake, the relevant pollen source area of Rockforest Lough is likely to be about 300-800 m, sampling pollen largely from extralocal sources, with some representation of local and regional sources. These patterns can be differentiated by comparison with other sequences from the area (Jacobson & Bradshaw, 1981; Sugita, 1994). The pollen profile from Rockforest Lough is similar in many respects to other profiles from the Burren, indicating that it records regional pollen signals. For example, it records the same open pinewood with *Corylus* described from Gortlecka and Rinn na Mona (Watts, 1984a) and Cappanawalla (Feeser & O'Connell, 2009). It also registers the Late Iron Age Lull and increased farming activity during the early medieval period, as described from Molly's Lough (Lamb & Thompson, 2005) and Lios Lairthín Mór (Jeličić & O'Connell, 1992). However, it was also possible to distinguish certain distinctive patterns in the extralocal vegetation. These include markedly elevated *Pinus* values throughout the study period, unusually high levels of arboreal pollen prior to the Great Famine of 1845 and the covariance of the *Fraxinus* and *Ulmus* pollen spectra.

### 3.5.4 Dynamics of *Pinus*

*Pinus* was thought to have become extinct in Ireland during the early medieval period, as the last unequivocal specimen of indigenous *Pinus* was recorded from Clonsast Bog at 1550 ± 140 cal BP (AD 410) (McAulay & Watts, 1961). The most striking feature of the Rockforest Lough profile is the absence of a *Pinus* decline. Not only is the *Pinus* curve continuous but the values are consistently high, never dropping below 38% of total terrestrial pollen. These values greatly exceed the 20% and subsequent 5% critical pollen percentages commonly used in determining the local presence of *Pinus* (Bennett, 1984, 1995). Furthermore, the presence of *Pinus* macrofossils shows conclusively that *Pinus* was locally present around Rockforest Lough. A *Pinus* needle was recovered at 1110 ± 60 cal BP (AD 840) and a *Pinus* wood fragment at 5810 ± 60 cal BP (3860 BC).

The *Pinus* macrofossil from Rockforest Lough at 1110 ± 60 cal BP (AD 840) is consistent with the 1050 ± 160 cal BP (AD 900) date for the last recorded *Pinus* pollen and macrofossils at Gortlecka (Watts, 1984a). This suggests that Watts' date was correct and that, at the time of its publication, the Gortlecka profile (and therefore the Burren, rather than midland raised bogs) supported Ireland's last known native population of *P. sylvestris*.

The Rockforest Lough profile is unique among Irish pollen diagrams in its continuous representation of very high levels of *Pinus* during the period when the species was considered to have been extinct in Ireland. There are several possible explanations for this unusual pattern. These include inaccurate dating, the long distance transport of *Pinus* pollen from extant populations elsewhere, redeposition of pollen in the lake sediment, inwash of eroded sediments containing *Pinus* pollen, contamination of sediment lacking *Pinus* pollen with either younger or older sediment containing abundant *Pinus* pollen and local persistence of a relict population of *P. sylvestris*.

The dating of the core seemed to be satisfactory (Fig. 3.4). It is acknowledged that a single AMS date was anomalously old (Table 3.1). Although we endeavoured to use terrestrial plant macrofossils for dating purposes by hand-picking or sieving them from the sediments, this bulk sample of unidentifiable organic material may have contained aquatic plant matter which, in this limestone region, would be susceptible to the hard water effect and would result in an anomalously old date. With this date excluded, the age-depth curve is smooth. This, taken with the homogeneous stratigraphy of the sediment, argues against the occurrence of a hiatus. The chronologies of the RFB and RFC cores matched well. The correlation of pollen markers, such as the rational limit of *Fagus* and the Late Iron Age Lull, with the dates provides further reassurance regarding the reliability of the chronology.

It is highly unlikely that long distance pollen input would swamp the extralocal component to such a degree. Although Tipping (1989) demonstrated that in an open, late glacial landscape in western Scotland, *Pinus* pollen frequencies arising from long distance transport could reach 40% of total terrestrial pollen, this study represents a less exposed, late Holocene landscape with high levels of internal pollen productivity. Furthermore, such an effect would have a similar impact on other pollen profiles in the region.

Due to the dynamic hydrogeology associated with karst landscapes, sediments in these areas are prone to redeposition or reworking of their stratigraphical order. Redeposition could have occurred at Rockforest Lough if, for example, the lake basin dried out and reflooded. This would have the effect of dampening sharp changes in the pollen profile. Although the curves of many of the taxa represented in Figure 3.5 are unusually stable, this is not thought to be due to redeposition. As a permanent lake, Rockforest Lough was selected for sampling partly because it was less likely to be subject to hiatuses and redeposition than the nearby turloughs. The core was taken from a deep basin (7.48 m) where, in living memory at least, the water level has been relatively stable (J. Cunningham, pers. comm.). The

stratigraphy of the relevant core section consisted of a homogeneous, cohesive brown algal mud with no evidence, such as a layer of carbonate clay, to indicate that a hiatus had occurred. The smooth chronology of the core also indicated that the stratigraphy has not been reworked. In addition, while the pollen curves of many of the taxa represented in Figure 3.5 were somewhat flat, the loss on ignition curve (Fig. 3.2) showed considerable variation.

Inwash of eroded sediment is typically associated with mountain lakes with catchments containing eroding upland blanket bog (Bradshaw & McGee, 1988; Leira *et al.*, 2007). Although the proportion of damaged or indeterminate pollen is rather high, Rockforest Lough is situated in the Burren lowlands and its catchment includes few, if any, extensive areas of peat. The section of lake sediment being examined in this study consisted of a homogeneous, cohesive brown algal mud, with no significant amounts of peat detritus. Inwashed eroded sediments would also result in anomalously old AMS dates which, with one exception, was not the case. In any case, the pollen input from inwashed eroded sediment would be unlikely to be profuse enough to produce such a consistently elevated *Pinus* signal.

The most likely way in which pollen sample contamination could occur in this case would be the contamination of sediment lacking *Pinus* pollen with either younger or older sediment containing abundant *Pinus* pollen. Extreme care was taken to minimise this source of error, both in the field and the laboratory. Again, in any case, this type of contamination would be unlikely to account for such consistently high *Pinus* values.

Consequently, the pollen profile from Rockforest Lough is thought to provide a true record of the surrounding vegetation over the last two millennia. From Figure 3.5, it seems that a relict population of *P. sylvestris* may have persisted in the immediate vicinity of Rockforest Lough from at least 2000 cal BP (50 BC) to the present day. A *Pinus* macrofossil recovered at 1100 cal BP (AD 850) provides convincing evidence of the local presence of the species (Froyd, 2005) and

coincides with a *Pinus* pollen frequency of about 45%. Although no further *Pinus* macrofossils were recovered after this time, the pollen record shows no evidence of any significant decline in the abundance of *Pinus*. *Pinus* was strongly represented in the pollen profile prior to the plantation of the Rockforest Estate, so although the planting included *Pinus* (Dutton, 1808), it is not thought to be the source of the present day pinewood at Rockforest. The most likely source of this pollen signal is therefore the pinewood at Rockforest, which is located about 500 m upwind of Rockforest Lough and is of the open, species-rich type described in the palaeoecological reconstruction.

The *Pinus* pollen signal is the main component of the sustained high values of arboreal pollen observed throughout the study period (Fig. 3.5). *P. sylvestris* pollen is usually abundantly produced, wind-borne and well dispersed (Bradshaw, 1981). This, taken with the apparent persistence of a pinewood upwind of and in close proximity to the pollen sampling site accounts for the unusually high values of arboreal pollen prior to the Great Famine of 1845.

Pollen analyses from some other sites in the region provide support for this hypothesis. In a meta-analysis of 84 dated, regional pollen cores, a set of isopoll maps were produced showing *Pinus* pollen frequencies in Ireland at 500 year intervals throughout the Holocene (Chapter 2). The interpolated isopoll maps depict an area of high *Pinus* pollen frequencies in western Ireland during the period when *Pinus* was thought to be extinct in Ireland (Figs. 2.3 t-w). This area is centred on Rockforest Lough, which was included in the analysis, but Lough Namackanbeg in south Connemara, 40 km to the north-west, also exhibited *Pinus* pollen frequencies of about 8-12.5% from 2000-500 cal BP (O'Connell *et al.*, 1988), although it must be noted that these frequencies are based on a total arboreal pollen sum. In addition, two undated pollen cores from the Burren exhibited low but continuous *Pinus* values throughout their upper halves. These were taken from the Carron Depression (Crabtree, 1982) and Rinn na Mona (Watts, 1984a), about 8 km north-west and 6 km west of Rockforest Lough

respectively (Fig. 3.1). These low values may represent the persistence of *Pinus* within the Burren region, at Rockforest for example, but not in the immediate vicinity of these sites. Where *Pinus* pollen signals have been recorded 'in the wrong place at the wrong time', the presumed extinction of *Pinus* in Ireland has led authors to account for the aberrant pattern by questioning the validity of their dating analyses (Watts, 1984a) or suggesting that redeposition or long distance transport may have occurred (Crabtree, 1982). It may be necessary to reinterpret such studies in light of the findings presented here.

### 3.5.5 Modern Analogues

During the early Holocene, the limestone pavement around Gortlecka is known to have supported open woodland composed of *Pinus*, *Corylus*, *Ulmus* and *Betula* (Watts, 1984a). Feeser and O'Connell (2009) found that open, species-rich pinewoods with *Corylus* dominated the uplands of the north-west Burren from about 3700-2570 cal BP (1750-620 BC). Similarly, pollen evidence indicates that the yew wood on limestone pavement at Reenadinna in County Kerry developed from woodland previously rich in *Pinus*, *Corylus*, *Quercus* and *Ulmus* at about 5730 cal BP (3780 BC) (Mitchell, 1990). The pollen evidence presented here suggests that this vegetation type has been represented continuously at Rockforest from at least 2000 cal BP (50 BC) to the present day. Furthermore, Feeser and O'Connell (2009) described this vegetation type as having floristic affinities to Scandinavian open pinewoods on calcareous soils. In a comparison of present-day Irish pinewoods with their European counterparts, close affinities were found between the woodland at Rockforest and Fennoscandian basiphilous pine forests (Chapter 5). The pinewoods on limestone pavement in the east Burren and Counties Galway and Mayo seem to be modern analogues of a vegetation type that has occupied the Burren and other karstic areas in Ireland since the early Holocene.

## 3.6 Conclusions

The pollen record from Rockforest Lough indicates a relatively stable vegetation history over the last two millennia, despite considerable human activity in the area, including partial woodland clearance, mixed farming and forestry. Woodland cover seems to have been continuous throughout the study period, although some reductions were recorded. The dominant vegetation type appears to have been an open pinewood with abundant *Corylus*, some *Betula* and occasional *Ulmus* and *Quercus*. Woodland cover was incomplete however, with open areas containing grassland and heathy vegetation. The record opened during the Late Iron Age Lull, when high levels of arboreal pollen indicate woodland regeneration and a low intensity of farming activity. This was followed by increased farming activity in the early medieval period, with a reduction in woodland cover and an expansion of open ground, particularly grassland. From the medieval period to the mid-nineteenth century, a gradual increase in arboreal pollen input is recorded. This pattern contrasts with the heavily deforested landscape represented in pollen diagrams from elsewhere in Ireland, particularly during the eighteenth and nineteenth centuries. It may be attributed to management practices on the Rockforest Estate, where plantations were being established while elsewhere poorer land was being cleared to make way for farmland to support the growing population. Increased mineral input from 610-100 cal BP (AD1340-1850) indicates increased human activity in the lake catchment and this corresponds to recorded events in the locality, such as the building of Rockforest House adjacent to the lake in the late eighteenth century. The period after the Great Famine of 1845 is characterised by relative instability and intense human activity. High levels of mineral input to the lake and an overall decline in arboreal pollen are accompanied by increased *Corylus* values and a peak in *Fraxinus*, indicating increased woodland exploitation or clearance. The rational limit of *Fagus* at 50 cal BP (AD 1900) marks the maturation of plantations on the Rockforest Estate. Meanwhile, the area of open ground, particularly grassland, continued to increase

up to the present day. Documentary sources such as maps and the historic literature and also local people's knowledge of the oral history of the area proved helpful in supplementing the palaeoecological proxies analysed.

What is remarkable about the pollen record from Rockforest Lough is the absence of a *Pinus* decline. *Pinus* macrofossils demonstrate the local presence of the species around the sampling site at 1100 ± 60 cal BP (AD 850) and *Pinus* pollen is represented continuously from 2000 cal BP (50 BC) to the present day at values consistently in excess of 38%. This suggests that a relict population of *P. sylvestris* persisted in the Burren during the period when this species was previously though to have become extinct in Ireland and has survived to the present day. The pinewood at Rockforest is the most likely source of this pollen signal and is a modern analogue of the pinewoods on limestone that have been present in Ireland since the early Holocene.

The implications of these findings are wide-ranging and significant. The research presented here strongly suggests that the widely accepted hypothesis that *Pinus* became extinct in Ireland is incorrect. If so, the significant body of palaeoecological research into the postglacial dynamics of *Pinus* in Ireland should be reviewed in the light of these findings. Although it is acknowledged that reintroduced populations of *P. sylvestris* cannot be considered as being genetically native, the species itself should be considered as native to Ireland. Relevant conservation and forest management policies should be reviewed accordingly. Finally, the pinewood at Rockforest should be the subject of further intensive research and conservation efforts. A similar pollen study of an adjacent lake (Plate 3.2) is proposed in order to further test the hypothesis of the continued survival of *P. sylvestris* in the Burren through the late Holocene. Additional future research could include palaeoecological analyses of other proxies, comparison of observed patterns with modelled pollen dispersal in the landscape surrounding the pinewood at Rockforest, molecular analyses of the population to determine its origin and ecological surveys of different taxa to establish the biodiversity value of the site.

# 4. Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland

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Plate 4.1. Photograph of a naturalised pinewood on the shore of Muckross Lake, Killarney, County Kerry with Torc Mountain in the background.

## 4.1 Abstract

Plantation forests can make a significant contribution to the conservation of native biodiversity, especially where native forest cover is low. Ireland is used as a case study to explore the contribution to biodiversity made by stands of *Pinus sylvestris* (Scots pine), a reintroduced species. Despite its disputed native status, *P. sylvestris* is being widely planted in semi-natural habitats in Ireland. The associated vegetation communities have not previously been described and their conservation value is unknown. Baseline information is needed to inform conservation and forest management strategies.

Botanical surveys were carried out at 20 plots of *P. sylvestris*-dominated woodland and scrub throughout the Republic of Ireland. Vegetation, structural and environmental data were recorded. Data were analysed using non-parametric and multivariate statistical techniques and a synoptic table was prepared.

*P. sylvestris* was found to be a non-specialist in terms of its environmental tolerances. $\beta$ diversity among plots was high while $\alpha$ diversity within plots was low to moderate. The plots surveyed contained 14.2% of the Irish native flora. There was a low level of constancy of species. Four reasonably well defined vegetation communities were identified. Soil pH, altitude and slope had important roles in partitioning these vegetation types and soil pH was positively correlated with species richness.

*P. sylvestris* is well established, well integrated and naturalising in Irish semi-natural habitats. Some of the associated vegetation communities corresponded to habitats of international conservation importance. This research demonstrates that stands of *P. sylvestris* represent an important resource for Ireland's native botanical and habitat diversity.

## 4.2 Introduction

There is currently considerable debate regarding the role played by plantation forests in contributing to biodiversity maintenance and enhancement (Hartley, 2002; Stephens & Wagner, 2007; Brockerhoff *et al.*, 2008). This is particularly significant in some European countries, where the area of plantations exceeds the area of native forests. In Denmark and the United Kingdom, for example, plantations constitute 63.0% and 67.6% of forest cover respectively. In Ireland, a very low proportion (9.7%) of the land area is covered by forest and a very high proportion (86.5%) of this is comprised of plantations (FAO, 2007). In situations where native or semi-natural woodland is so scarce, and particularly where Sustainable Forest Management is applied, non-native plantations assume importance as a resource for biodiversity (Brockerhoff *et al.*, 2008). Due to its island status, small size and low coverage of native woodland, Ireland is a model study site for investigating the contribution that non-native, or questionably native, tree species can make to the conservation of native biodiversity. Ireland's native botanical diversity is considerably lower than elsewhere in northwest Europe. This disparity is a product of Ireland's small size, island status, glacial history and its position at the edge of Europe. Excluding Pteridophytes, apomicts, doubtfully native species and other critical taxa, the vascular flora amounts to just 815 species (Webb, 1983). Ireland provides an interesting, and previously undescribed, ecological case study of *Pinus sylvestris* at the western limit of its range.

*P. sylvestris* or Scots pine is the most widely distributed pine species in the world (Vidakovic, 1991). Its native range covers approximately 2,700 km north to south and 14,000 km east to west across Asia and Europe (Volosyanchuk, 2002). *P. sylvestris* is widely but discontinuously distributed within these limits (Steven & Carlisle, 1959). This wide geographic range reflects the species' tolerance of a wide range of climatic conditions. *P. sylvestris* forms stable vegetation communities on nutrient-deficient soils, indicating a high competitive ability under these conditions (Carlisle & Brown, 1968). It may act as a pioneer species,

particularly on raised bogs which have suffered drainage or disturbance (Stoll *et al.*, 1994). However, it is light demanding and will not tolerate heavy shade from other trees (Carlisle & Brown, 1968). *P. sylvestris* forms vegetation communities of international conservation importance. For example, *P. sylvestris* is the dominant tree species in the Western Carpathian calcicolous *P. sylvestris* forests of Eastern Europe and the Caledonian forests of Scotland, both of which are listed on Annex I of the European Union Habitats Directive (EEC, 1992). In addition, *P. sylvestris* is one of the most commercially important Eurasian forest trees (Volosyanchuk, 2002).

What is particularly intriguing in this case is that indigenous *P. sylvestris* was once widespread in Ireland but is believed to have been extirpated and subsequently reintroduced. Palaeoecological evidence indicates that, following deglaciation, *P. sylvestris* colonized Ireland by 9500 BP (radiocarbon years before present) (Mitchell, 2006). It expanded its range and by 7500 BP, had become an important component of certain marginal habitats, such as raised bogs, river valleys and uplands. Indeed, *P. sylvestris* was the dominant tree pollen type in almost all western and most upland study sites for at least part of the early post-glacial (Bennett, 1984; Bradshaw & Browne, 1987). These are mainly areas of acidic rock, but there is evidence that *P. sylvestris* also grew on the karst limestone pavement of the Burren (Watts, 1984a). A major *P. sylvestris* decline began around 4000 BP. The decline was asynchronous (Smith & Pilcher, 1973) and may have been caused by a combination of different factors in different parts of Ireland. Competition with *Alnus glutinosa*, the expansion of blanket bog, climate change, progressive soil deterioration, pathogens and human activity have all been cited as possible causes of the decline (Bennett, 1984). Late outposts of *P. sylvestris* persisted in Sligo, the Killarney valley, the Burren and on raised bogs in the Midlands (Bradshaw & Browne, 1987). The most recent unequivocal specimen, a preserved stump from Clonsast Bog in County Offaly, was radiocarbon dated to 1,620 ± 130 BP (McAulay & Watts, 1961). *P. sylvestris* is widely believed to

have become extinct in Ireland at this point (White & Doyle, 1982; Webb *et al.*, 1996; Cross, 1998).

Native *P. sylvestris* woodland persists to the present day in Britain, but is restricted to the Scottish highlands, where it dominates considerable areas (Steven & Carlisle, 1959). These Caledonian forests are now recognised as a priority habitat under Annex I of the EU Habitats Directive (NATURA 2000 code 91C0) (EEC, 1992). The species had been reintroduced to Ireland by the eighteenth century AD, probably from Scotland. Pococke (1891) observed a thriving plantation of 20,000 "firres" near Coolnamuck, Carrick-on-Suir, County Tipperary in 1752. A documented reintroduction took place at Killarney, County Kerry around 1800 when *P. sylvestris* of Scottish provenance was planted extensively on the Kenmare and Herbert Estates (Radcliff, 1814; Watts, 1984b). This sequence of regional extinction and reintroduction of *P. sylvestris* is also thought to have occurred in Belgium, Denmark, the Netherlands, England and Wales (Mirov, 1967; Bennett, 1984; Bradshaw, 1993; Le Maitre, 1998; Lust *et al.*, 2000) (Fig. 1.1).

Since its reintroduction, *P. sylvestris* has been widely planted in Ireland (Cross, 1998) and is naturalising in a variety of habitats (Kelly, 1981, 1985) (Plate 4.1). Earlier in the twentieth century, extensive plantations of *P. sylvestris* were established but after 1945, more productive exotic species, especially *Picea sitchensis*, became favoured for commercial forestry (O'Driscoll, 1980). *P. sylvestris* is regarded as 'semi-native' within the Irish forestry sector and is Ireland's only native or semi-native conifer species with forestry potential (Forest Service, 2000). Ireland's Native Woodland Scheme provides grant aid to landowners for the planting of native tree species of local genetic provenance (Forest Service, 2001). Despite its disputed native status, *P. sylvestris* has been included in this scheme and is being widely planted in semi-natural habitats. Information is therefore urgently required on the plant community ecology of *P. sylvestris* stands and the implications for biodiversity conservation.

Despite its widespread distribution, very few published studies provide vegetation descriptions or classifications applicable to *P. sylvestris* in Ireland. This inadequate description is a product of the species' disputed native status and declining popularity in commercial forestry. *P. sylvestris* woodlands were excluded from the Irish National Survey of Native Woodland and its associated classification of vegetation communities (Perrin *et al.*, 2006; Perrin *et al.*, 2008b, a). White's (1982) key for the identification of Irish plant communities ascribes all coniferous woodland to the Vaccinio-Piceetea class. However White & Doyle (1982), in an overview of phytosociological associations in Ireland, argued that there are no native *P. sylvestris* woodlands in Ireland and did not formally record the class. Fossitt's (2000) broad-scale classification of Irish habitats made some provision for *P. sylvestris* woodland. All coniferous plantations were ascribed to the highly modified/non-native woodland class and sub-divided, regardless of ground flora, into mixed broadleaved/conifer (WD2), mixed conifer (WD3) and conifer (WD4) categories. In the semi-natural woodland class, the bog woodland (WN7) category was defined on the basis of species composition and referred to woodlands of intact ombrotrophic bogs, bog margins and cutover bog. *Betula pubescens* is the usual dominant but some stands on intact raised bog are dominated by *P. sylvestris* (O'Connell & Doyle, 1990; Heery, 1993). Bog woodland is a priority habitat under Annex I of the EU Habitats Directive (91D0) (EEC, 1992) and examples on intact raised bog are very rare in Ireland (Fossitt, 2000). Quantitative data on the vegetation communities of *P. sylvestris* stands are required. In this paper we describe naturalised and planted stands of *P. sylvestris* and assess their contribution to Ireland's native biodiversity.

## 4.3 Methods

### 4.3.1 Site Selection

The site selection criteria stipulated mature woodland or scrub composed of pure *P. sylvestris* or *P. sylvestris* intimately mixed with native tree species, with *P. sylvestris* as a dominant or co-dominant in the canopy. The vegetation had to be reasonably free of non-native and/or invasive species. Planted and naturalised stands and those of unknown provenance were included. Relevant stakeholders were consulted and a desk study was carried out to identify potential survey sites in both the Republic of Ireland and Northern Ireland. After preliminary visits, several sites that failed to meet the selection criteria were rejected. This was due, in part, to invasion by the non-native *Rhododendron ponticum*, which was particularly pernicious in the south-west of the country. Eighteen suitable sites were selected according to the criteria outlined above. We are satisfied that although this survey was not exhaustive, it covered an adequate proportion of the *P. sylvestris* woodlands that would meet the site selection criteria.

### 4.3.2 Data Collection

Field surveys were conducted from May - September 2006 and from April - August 2007. Twenty plots were surveyed at eighteen sites (Table 4.1, Fig. 4.1), as two distinct *P. sylvestris*-dominated vegetation types occurred at the Derrycrag and Ballykine sites. A circular 400 $m^2$ plot was subjectively placed to represent each *P. sylvestris* vegetation type. The circular shape facilitated a study of pollen dispersal, which is not presented here. As shown in Roche *et al.* (2008, Appendix 4.1), five 2 x 2 $m^2$ quadrats were placed within the 400 $m^2$ plot, with one at the centre and at each of the cardinal points. This quadrat size was chosen to capture vascular ground flora diversity, where the dominant structural form varied from herbs to sub-shrubs. In each of these quadrats, floristic data were recorded on the Domin scale (Dahl & Hadac, 1941) for woody species and herbs. Bryophyte data were recorded on a presence/absence basis. Nomenclature followed Webb *et al.* (1996) for vascular plants, Smith (2004) for mosses and Hill *et al.* (2008) for liverworts. Structural data were recorded for all live trees within the plot with a

diameter at breast height (DBH) of 7 cm or greater. DBH was measured using a diameter tape. The height of the tallest tree was estimated using a clinometer and the heights of the remaining trees were then estimated by eye. Each tree was ascribed to a structural class: dominant, co-dominant, intermediate or suppressed. The slope, altitude and Irish Grid coordinates of the plot were recorded. In each 4 $m^2$ quadrat, five 10 cm deep soil samples were taken and bulked in the field. Soil pH was determined in the laboratory using a WTW pH 330 meter and combination electrode. Soil organic content was determined by % loss on ignition at 550$^o$ C. Approximate soil bulk density was estimated from % organic content (Jeffrey, 1970).

Table 4.1. Location of the 20 survey plots shown in Figure 4.1.

| Plot Number | Plot Name | County | Irish Grid Reference |
|---|---|---|---|
| 1 | Dale Wood | Kerry | V 88181 80714 |
| 2 | Clonfinane Bog | Tipperary | M 98815 03715 |
| 3 | Rockforest | Clare | R 34755 95013 |
| 4 | Priest's Leap | Cork | V 98853 59132 |
| 5 | Glengarriff | Cork | V 90894 56831 |
| 6 | All Saints Bog | Offaly | N 01203 11216 |
| 7 | Glenfarne | Leitrim | H 02059 39747 |
| 8 | The Scalp | Dublin | O 21719 20093 |
| 9 | Coronation Plantation | Wicklow | O 09708 12792 |
| 10 | Derrycrag plot 1 | Galway | R 73616 99077 |
| 11 | Derrycrag plot 2 | Galway | R 73652 99029 |
| 12 | Portumna Forest Park | Galway | M 82680 03320 |
| 13 | Rockvale | Clare | R 38955 98090 |
| 14 | Torc | Kerry | V 96482 83719 |
| 15 | Knockastakeen | Tipperary | R 93807 27204 |
| 16 | Trooperstown | Wicklow | T 15932 96721 |
| 17 | Derrybawn | Wicklow | T 12365 96360 |
| 18 | Vale of Clara | Wicklow | T 17212 92127 |
| 19 | Ballykine plot 1 | Mayo | M 10849 57328 |
| 20 | Ballykine plot 2 | Mayo | M 10657 57113 |

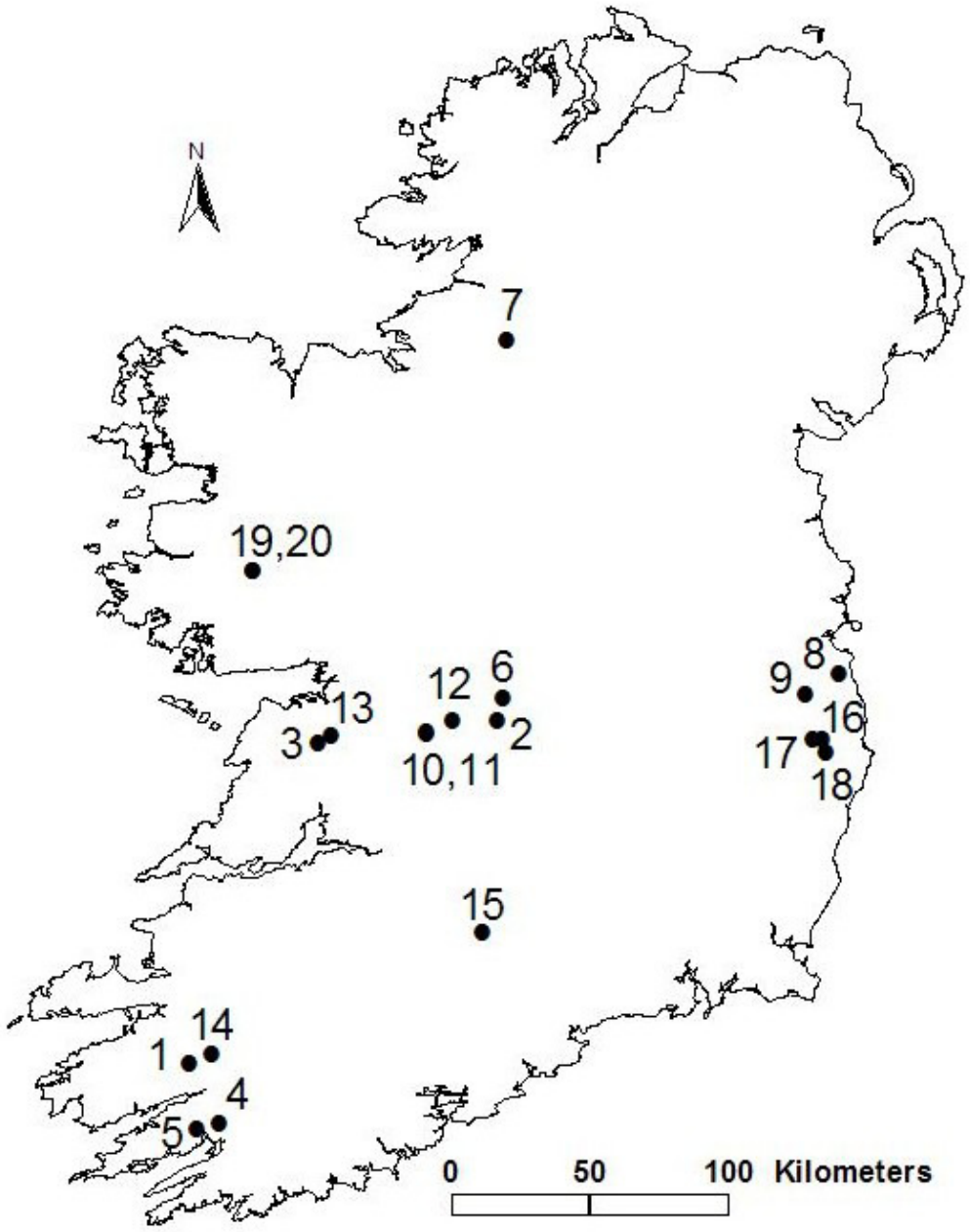


Figure 4.1. Location map of the 20 survey plots listed in Table 4.1.

### 4.3.3 Data Analysis

The diversity of vascular plant species was calculated at two scales, α diversity (from five 4 $m^2$ quadrats within each plot) and β diversity (from 20 400 $m^2$ plots throughout Ireland). Whittaker's index of β diversity was applied at both the α and β scales, using the following formula:

$\alpha$ or $\beta = (S_C/S_A)-1$

$S_C$ is the species richness in the composite sample and $S_A$ is the average species richness in the sample units (Whittaker, 1960, 1972; McCune & Grace, 2002). This index was selected as it is one of the simplest and most effective measures of spatial diversity. It is essentially a measure of the extent to which two or more sample units differ (Magurran, 2004) and was therefore an appropriate measure of diversity at both the α and β scales.

The nested sampling design provided floristic data from five 4 $m^2$ quadrats within each plot. Abundance data for vascular plants were recorded on the Domin scale. As bryophyte data were recorded in presence/absence format only, they were not included in the multivariate analysis of floristic data. Ordinal Domin scores are incompatible with many conventional multivariate analysis techniques. The conversion of ordinal scores to mean values of percentage cover classes implied arbitrariness and non-systematic distortion and would produce a considerable increase in the uncertainty of the data (Podani, 2006). Preliminary analyses showed that α diversity was low relative to β diversity so, for the purposes of this paper, the patterns of β diversity were deemed to be of greater interest than those of α diversity. Given the relative homogeneity of the quadrats within each plot, it was decided that their floristic data could be combined into robust summary data which would describe the 400 $m^2$ plot at the stand scale. The Domin values were transformed to estimates of percentage cover using Currall's (1987) 'Domin 2.6' method, which is more accurate than direct averaging. A mean of the resulting values was calculated, providing summary data at the scale of the 400 $m^2$ plot.

The mean values were reconverted to the Domin scale, thereby reducing uncertainty in the data i.e. the false accuracy of percentages that actually represent a range of values. This data format was thought to be the most defensible option given the sampling design used, however it was incompatible with certain data analysis techniques such as Indicator Species Analysis (Podani, 2006).

Data screening, data transformation and multivariate data analyses were carried out using PC-ORD 5 (McCune & Mefford, 2005). Data were screened by Outlier Analysis. None of the plots were identified as outliers and all were included in the analysis. *Succisa pratensis* was identified as a marginal outlier (SD = -2.12) but was retained in the dataset, as the species is part of the target population. Rarely occurring species, i.e. those that occurred in only one (5%) of the plots, were deleted to reduce noise in the dataset (McCune & Grace, 2002). A hierarchical, agglomerative, polythetic method of Cluster Analysis was used for classification. Sørensen's (Bray-Curtis) distance measure was used with the Flexible Beta linkage method, with parameter $\beta$ set at -0.25 (Lance & Williams, 1967). The dendrogram was scaled by the objective function, which is widely applicable and relatively informative. Nonmetric Multidimensional Scaling (NMS) was used for ordination and was run from a random starting configuration in slow and thorough autopilot mode, with Sørensen selected as the distance measure. The stability criterion was set at 0.00001 and the number of iterations to evaluate stability was set at 15. A Monte Carlo test was carried out with 250 randomized runs. The similarity of plots was assessed by the identification of natural groups on the cluster dendrogram and verified with reference to the structure of NMS ordinations.

Histograms and normal probability plots showed that the environmental data did not fit the normal distribution and were incompatible with parametric statistics (Kent & Coker, 1992). The non-parametric Spearman's rank correlation coefficient was calculated for environmental variables, species richness and ordination scores using Data Desk 6.1 (Velleman, 1997).

In order to describe the species composition of these groups, floristic data were sorted in a synoptic table following the style of the British National Vegetation Classification (Rodwell, 1991b). Frequency and abundance values for each species, within each group and overall, are presented. Frequency classes are denoted by Roman numerals as follows: 1-20% = I, 21-40% = II, 41-60% = III, 61-80% = IV, 81-100% = V. The terminology used also followed Rodwell (1991b). Constant species are those with an overall frequency of IV or V. General associates are those species with an overall frequency of III or less that do not show a marked affiliation to any particular group. Preferential species are distinctly more frequent within one or more of the groups than the others and differential species are those whose affiliation is exclusive to one group. The most strongly preferential species were used in naming the groups. Although the presence/absence format bryophyte data were not included in the multivariate analyses used to derive the groups, bryophyte frequency data are presented in the synoptic table to provide additional detail on the vegetation associated with each group and facilitate comparison with phytosociological syntaxa.

## 4.4 Results

Observations in the field have shown that *P. sylvestris* occupies a wide variety of substrates in Ireland including raised bog, limestone pavement and upland blanket bog.

### 4.4.1 Species Diversity

The dataset contained a total of 131 vascular plant species. According to McCune & Grace's (2002) rule of thumb, $\beta$ diversity values greater than five are considered high and less than one rather low. Thus, the overall $\beta$ diversity ($\beta = 5.57$) was high. The majority of plots exhibited low $\alpha$ diversity (Fig. 4.2), although Plots 20

(Ballykine plot 2) and 14 (Torc) approached moderate α diversity. The α diversity of individual plots was low in comparison with the overall β diversity.

Five species in the dataset, *Acer pseudoplatanus, Fagus sylvatica, Larix decidua, Picea sitchensis* and *Rhododendron ponticum*, are considered non-native in Ireland (Webb *et al.*, 1996). The native status of *P. sylvestris* is indeterminate. Following Webb's (1983) rationale, the removal of non-native species, Pteridophytes, apomicts, doubtfully native species and other critical taxa from the dataset yields a total of 116 native vascular plant species. The *P. sylvestris* plots surveyed represent 14.2% of the Irish native flora.

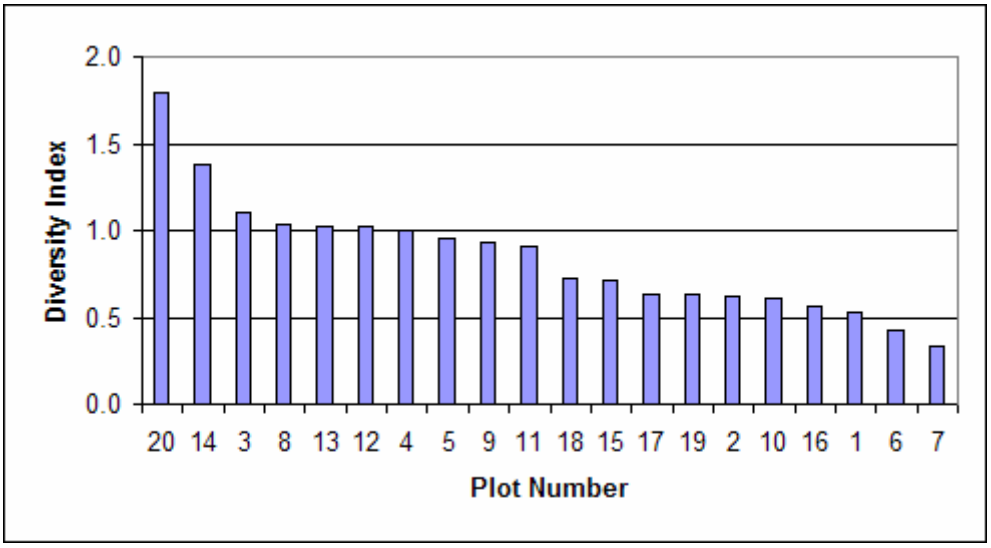


Figure 4.2. α-diversity within the 20 survey plots listed in Table 4.1.

### 4.4.2 Classification of Putative Vegetation Communities

During data transformation, the deletion of species occurring in only one plot removed 68 species, or 51.9% of the total. Cluster Analysis produced four natural groups (Fig. 4.3). NMS found a three-dimensional solution (Fig. 4.4) with a final stress of 12.7%, which indicated an intermediate solution according to Kruskal's

rule of thumb (McCune & Grace, 2002). A Monte Carlo test showed that the probability of a similar final stress being obtained by chance was 0.0080.

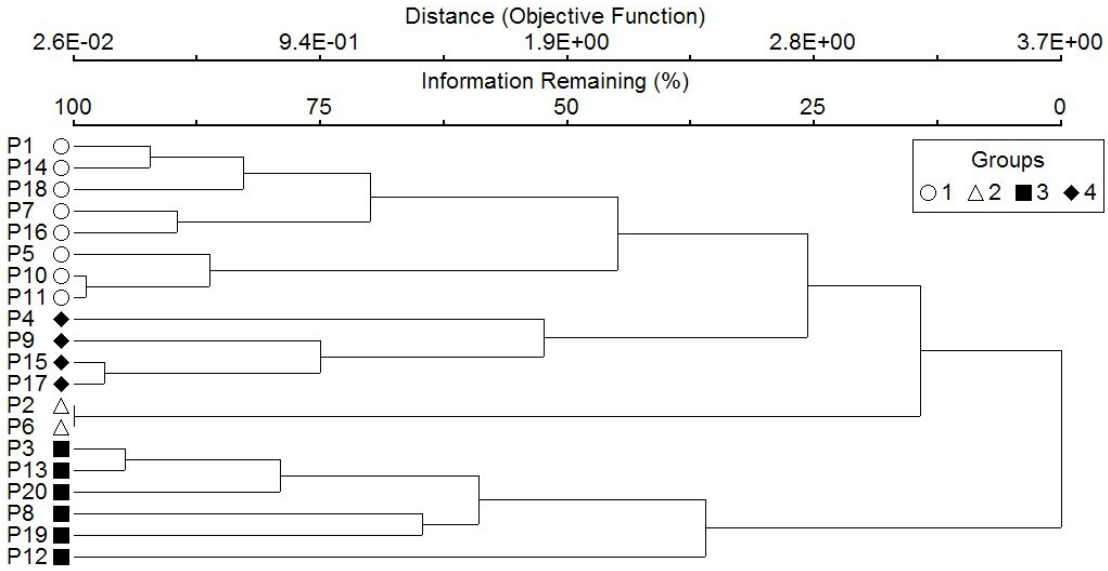


Figure 4.3. Cluster dendrogram of the 20 plots listed in Table 4.1, labelled with four natural groups.

The natural groups identified by cluster analysis corresponded to reasonably well defined areas on the NMS ordinations. Axis 1, which represented the largest proportion of variance in the data ($r^2 = 0.397$) (Fig. 4.4), exhibited an extremely significant positive correlation with soil pH (r = 0.708) (Table 4.2). This axis separated Group 3, so that it was defined by relatively high soil pH values. The remaining groups all exhibited low soil pH values (Fig. 4.4). Axis 3, which represented the second largest proportion of variance in the data ($r^2$ =0.208) (Fig. 4.4a), exhibited an extremely significant negative correlation with altitude (r = -0.713) (Table 4.2). This axis separated Group 4, so that it was defined by relatively low soil pH and high altitude. Axis 2, which represented the smallest proportion of variance in the data ($r^2 = 0.186$) (Fig. 4.4), exhibited a significant negative correlation with slope (r = -0.494) (Table 4.2). This axis separated the remaining groups. Thus, Group 1 was defined by relatively low soil pH and sloping topography and Group 2 by relatively low soil pH, low altitude and flat

topography (Fig. 4.4b). Species richness exhibits an extremely significant positive correlation with soil pH (r = 0.666) (Table 4.2).

Constant species are those with an overall frequency of IV or V (Rodwell, 1991b). In Irish pinewoods, the constant species are *P. sylvestris*, *Pteridium aquilinum*, *Hedera helix* and *Sorbus aucuparia* (Table 4.3).

(a)

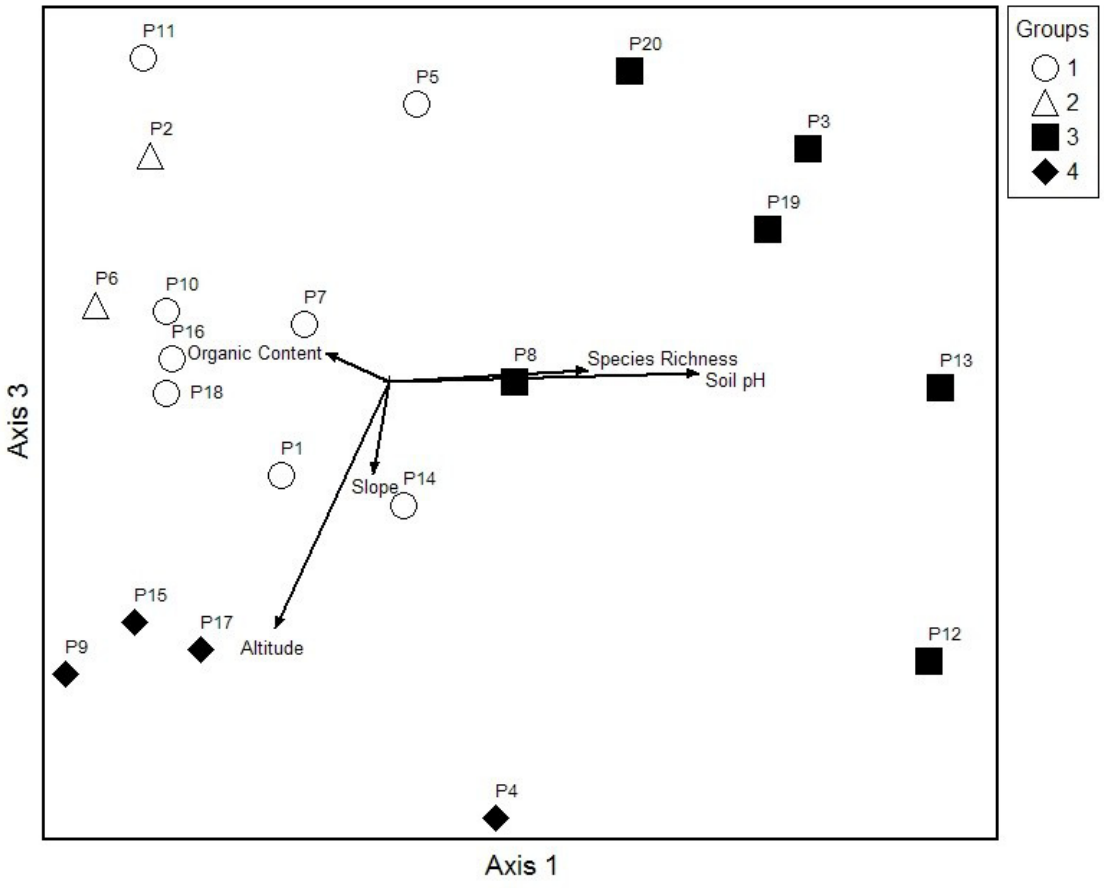


Figure 4.4 (a, b). Nonmetric Multidimensional Scaling ordinations of the 20 plots listed in Table 4.1., showing the four groups derived by cluster analysis and a biplot of environmental variables ($r^2$ values of axes: 1 = 0.397; 2 = 0.186; 3 = 0.208; Total = 0.792). (a) Axes 1 and 3 ($r^2$ = 0.605) and (b) Axes 1 and 2 ($r^2$ = 0.585).

(b)

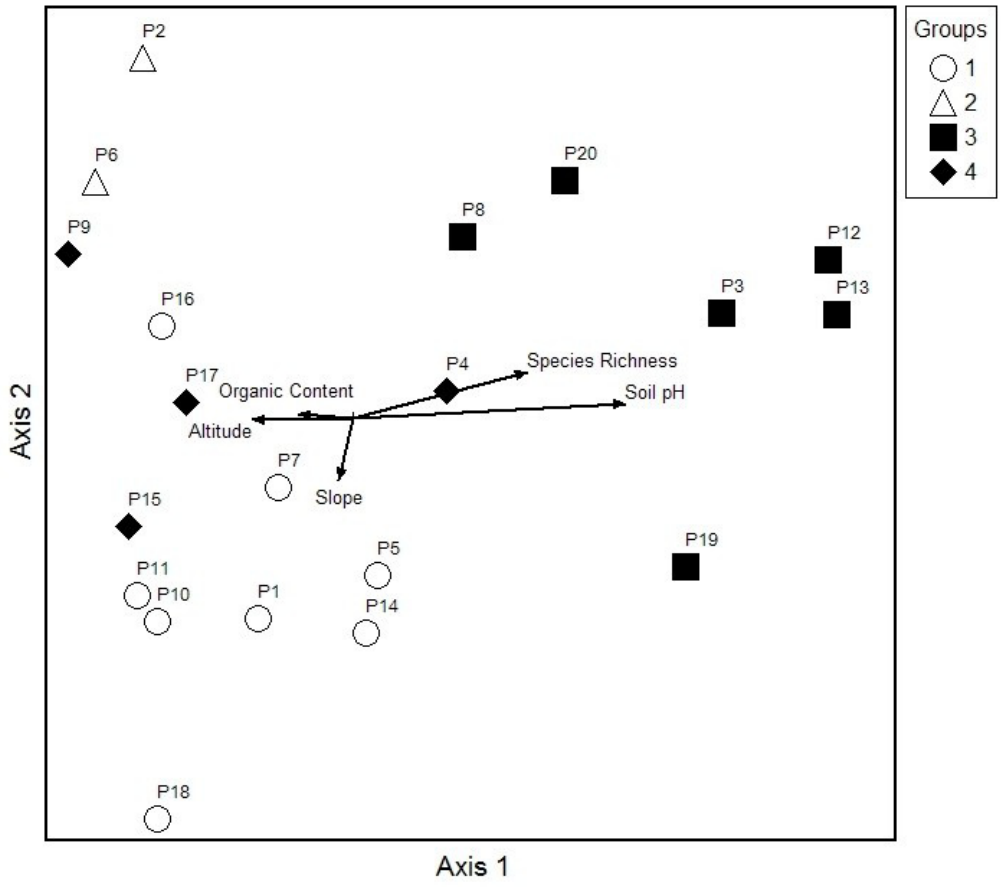
Groups
1
2
3
4
P2
P6
P9
P20
P8
P12
P3
P13
P16
P17
Organic Content
P4
Species Richness
Soil pH
Altitude
P7
Slope
P15
P19
P5
P11
P10
P1
P14
P18
Axis 2
Axis 1

Table 4.2. Spearman rank correlation coefficients for ordination scores, environmental variables and species richness.

| | Axis 1 | Axis 2 | Axis 3 | Soil pH | % Organic content | Bulk density | Slope | Altitude |
|---|---|---|---|---|---|---|---|---|
| Soil pH | 0.708*** | 0.075 | -0.08 | - | - | - | - | - |
| % Organic Content | -0.382* | 0.087 | 0.241 | -0.630** | - | - | - | - |
| Bulk Density | 0.373 | -0.072 | -0.234 | 0.627** | -0.999*** | - | - | - |
| Slope | -0.089 | -0.494* | -0.501* | 0.044 | -0.427* | 0.429* | - | - |
| Altitude | -0.552** | -0.181 | -0.713*** | -0.265 | -0.071 | 0.071 | 0.620** | - |
| Species Richness | 0.855*** | 0.309 | -0.069 | 0.666*** | -0.251 | 0.249 | -0.04 | -0.326 |

Statistically significant correlations are indicated: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

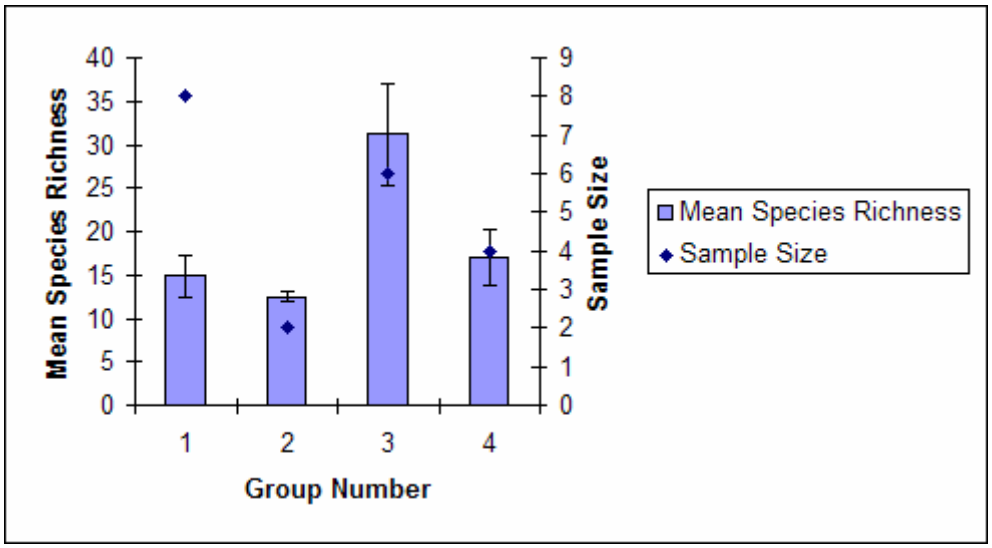


Figure 4.5. Mean vascular plant species richness (± standard error) and sample size of the four natural groups derived by cluster analysis.

*Group 1: Vaccinium myrtillus-Ilex aquifolium*

Sites: Dale Wood (1), Glengarriff (5), Glenfarne (7), Derrycrag Plot 1 (10), Derrycrag Plot 2 (11), Torc (14), Trooperstown (16), Vale of Clara (18), N = 8

This was the most frequent of the putative vegetation types (40% of plots). The preferential species included *Ilex aquifolium, Vaccinium myrtillus, Betula pubescens, Quercus petraea*, *Dryopteris dilatata*, *Hypnum andoi*, *H. cupressiforme*, *Isothecium myosuroides*, *Pseudotaxiphyllum elegans* and *Dicranum majus*. The differential taxa were *Rhododendron ponticum*, *Quercus* hybrids and *Plagiochila spinulosa*. This vegetation type consisted of relatively dense, high forest stands. The canopy was dominated by *P. sylvestris* with varying abundances of *Quercus*, chiefly *Q. petraea*. The understorey was dominated by *Ilex aquifolium*, with plentiful *Sorbus aucuparia* and *Betula pubescens*. The field layer was dominated by *Vaccinium myrtillus* with varying abundances of *Pteridium aquilinum*, *Hedera helix*, *Blechnum spicant*, *Luzula sylvatica* and *Rubus fruticosus* agg. (Table 4.3). The mean species richness of this vegetation type was

relatively low but was comparable with that of Groups 2 and 4 (Fig. 4.5). This vegetation type tended to occur on sites with acidic soils and sloping ground at moderate altitudes (Table 4.3).

*Group 2: Calluna vulgaris-Eriophorum vaginatum*

Sites: Clonfinane Bog (2), All Saints Bog (6), N = 2

This was the least frequent of the putative vegetation types (10% of plots). The preferential species included *Calluna vulgaris*, *Dicranum scoparium* and *Sphagnum palustre*. The differential species included *Andromeda polifolia, Empetrum nigrum, Erica tetralix, Eriophorum vaginatum, E. angustifolium, Vaccinium oxycoccus, Dryopteris carthusiana, Aulacomnium palustre, Sphagnum fimbriatum, S. magellanicum* and *S. squarrosum*. This vegetation type consisted of relatively dense stands. The canopy was quite low and was dominated by *P. sylvestris* with varying abundances of *Betula pubescens*. *B. pubescens* regeneration dominated the understorey. The field layer was dominated by *Calluna vulgaris* with plentiful *Eriophorum vaginatum*. *Empetrum nigrum, Erica tetralix, Andromeda polifolia, Vaccinium oxycoccus* and *Rubus fruticosus* agg. were present at low abundances (Table 4.3). This vegetation type exhibited the lowest mean species richness. However, as the sample size was relatively small and species diversity is likely to increase with the area or number of sites sampled, this assessment of relative diversity may not be statistically sound. In any case, the species richness values for both plots lay within a similar range to those of Groups 1 and 4 (Fig. 4.5). This vegetation type occurred only on raised bogs in the lowlands. These sites exhibited flat topography and waterlogged, acidic peat soils with a high organic content (Table 4.3).

*Group 3: Corylus avellana-Brachypodium sylvaticum*

Sites: Rockforest (3), The Scalp (8), Portumna Forest Park (12), Rockvale (13), Ballykine Plot 1 (19), Ballykine Plot 2 (20), N = 6

This was the second most frequent of the putative vegetation types (30% of plots). The preferential species included *Corylus avellana*, *Lonicera periclymenum*, *Anthoxanthum odoratum*, *Viola riviniana / reichenbachiana* and *Festuca ovina*. The differential species included *Crataegus monogyna*, *Fraxinus excelsior*, *Brachypodium sylvaticum*, *Prunus spinosa*, *Teucrium scorodonia* and *Ctenidium molluscum*. The structure of this putative vegetation type was heterogeneous, as it incorporated both high forest and scrub. Despite this, there was a certain consistency in the species composition of these plots. *P. sylvestris* was structurally dominant, forming a canopy in high forest stands and scattered standards in scrub. *Corylus avellana* generally dominated the understorey or shrub layer. *Fraxinus excelsior, Crataegus monogyna* and *Prunus spinosa* were also present at varying abundances. The field layer was variable but *Brachypodium sylvaticum, Hedera helix, Anthoxanthum odoratum, Lonicera periclymenum, Viola riviniana / reichenbachiana, Pteridium aquilinum, Festuca ovina,* and *Teucrium scorodonia* were constant species (Table 4.3). The mean species richness of this vegetation type was markedly higher than that of the other groups (Fig. 4.5). The habitats in which this vegetation type occurred were heterogeneous. Rockforest, Rockvale and Ballykine Plot 2 occur on limestone pavement. Portumna Forest Park and Ballykine Plot 1 occur on limestone-derived soils. The Scalp occurs on relatively acidic soil with granite outcrops. These sites are related by the presence of exposed or outcropping rock and/or relatively high soil pH. With the exception of The Scalp, they generally occur on gentle slopes in the lowlands (Table 4.3).

*Group 4: Galium saxatile-Agrostis capillaris*

Sites: Priest's Leap (4), Coronation Plantation (9), Knockastakeen (15), Derrybawn (17), N = 4

This was the third most frequent of the putative vegetation types (20% of plots). The preferential species included *Galium saxatile, Agrostis capillaries, Oxalis acetosella, Plagiothecium undulatum, Polytrichastrum formosum* and *Rhytidiadelphus loreus*. The differential species included *Agrostis vinealis* and *Holcus lanatus*, although these were only occasional even within this group. This vegetation type consisted of a relatively high but open canopy, which was completely dominated by *P. sylvestris*. The understorey was sparse or absent but, where present, it was dominated by *Sorbus aucuparia*. The field layer was variable but was generally dominated by combinations of *Pteridium aquilinum, Vaccinium myrtillus* and *Molinia caerulea*. *Galium saxatile, Blechnum spicant, Agrostis capillaris* and *Oxalis acetosella* were generally present at lower abundances (Table 4.3). The mean species richness of this vegetation type was intermediate (Fig. 4.5). The mean altitude of this vegetation type was markedly higher than that of the other groups. This vegetation type tended to occur on upland sites with acidic soils and sloping topography (Table 4.3).

## 4.5 Discussion

### 4.5.1 Spatial Diversity

The field surveys demonstrated that *P. sylvestris* occupies a wide variety of substrates in Ireland, displaying the broad edaphic and topographic amplitude described by Carlisle & Brown (1968). It is therefore a non-specialist in terms of its environmental tolerances. In terms of vascular plant species, $\beta$ diversity among plots was high while $\alpha$ diversity within plots varied from low to moderate. There was a low level of constancy of species within *P. sylvestris* stands in Ireland, which was demonstrated by the large proportion of species lost during the deletion of rare species (51.9%). This reflects variability and diversity in the species composition of *P. sylvestris* stands.

Table 4.3. Synoptic table of floristic and environmental data for the four groups derived by cluster analysis.

| **Group** | **1** | | **2** | | **3** | | **4** | | **Overall** | |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of Plots | 8 | | 2 | | 6 | | 4 | | 20 | |
| **Constant Species** | | | | | | | | | | |
| *Pinus sylvestris* | V | (5-8) | V | (7) | V | (4-7) | V | (7-8) | V | (4-8) |
| *Pseudoscleropodium purum* | IV | | V | | V | | V | | V | |
| *Thuidium tamariscinum* | V | | III | | V | | V | | V | |
| *Pteridium aquilinum* | IV | (+-7) | III | (7) | IV | (1-5) | IV | (3-7) | IV | (+-7) |
| *Hedera helix* | IV | (+-4) | III | (+) | V | (+-5) | III | (+-1) | IV | (+-5) |
| *Sorbus aucuparia* | V | (+-5) | | | II | (1-2) | V | (+-5) | IV | (+-5) |
| *Hypnum jutlandicum* | V | | V | | III | | IV | | IV | |
| **General Associates** | | | | | | | | | | |
| *Blechnum spicant* | V | (+-4) | | | | | V | (+-2) | III | (+-4) |
| *Rubus fruticosus* agg. | III | (+-4) | V | (+-1) | V | (1-4) | | | III | (+-4) |
| *Luzula sylvatica* | III | (3-7) | | | | | III | (+-1) | II | (+-7) |
| *Agrostis canina* | I | (1) | | | III | (+) | III | (1-3) | II | (+-3) |
| *Potentilla erecta* | II | (+-1) | | | III | (+-1) | III | (1-3) | II | (+-3) |
| *Brachythecium rutabulum* | III | | | | III | | | | II | |
| *Hylocomium splendens* | II | | III | | II | | III | | II | |
| *Lophocolea bidentata* | III | | III | | | | III | | II | |
| *Polytrichum commune* | I | | III | | | | III | | I | |
| *Polypodium vulgare* | II | (+-1) | | | II | (+) | | | II | (+-1) |
| *Quercus robur* | II | (3-4) | | | II | (1-5) | | | I | (1-5) |
| *Hypnum resupinatum* | II | | | | II | | | | I | |
| *Radula complanata* | II | | | | | | II | | I | |
| *Fagus sylvatica* | I | (3) | | | I | (1) | | | I | (1-3) |
| *Ulota bruchii* | I | | | | I | | | | I | |

**Group 1**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Preferential Species** | | | | | | | | | | |
| *Vaccinium myrtillus* | V | (1-8) | III | (2) | | | IV | (4-6) | III | (1-8) |
| *Ilex aquifolium* | V | (1-8) | | | III | (1-4) | II | (+) | III | (+-8) |
| *Betula pubescens* | V | (+-5) | V | (5-6) | I | (5) | II | (+) | III | (+-6) |
| *Quercus petraea* | IV | (+-6) | | | I | (4) | | | II | (+-6) |
| *Hypnum andoi* | IV | | III | | III | | III | | III | |
| *Hypnum cupressiforme* | IV | | III | | II | | II | | III | |
| *Isothecium myosuroides* | IV | | | | II | | II | | III | |
| *Pseudotaxiphyllum elegans* | IV | | | | I | | III | | II | |
| *Dicranum majus* | III | | | | II | | | | II | |
| *Kindbergia praelonga* | III | | | | II | | II | | II | |
| *Dryopteris dilatata* | II | (1-3) | | | I | (4) | | | I | (1-4) |
| *Frullania tamarisci* | II | | | | I | | | | I | |
| | | | | | | | | | | |
| **Differential Species** | | | | | | | | | | |
| *Quercus* hybrids | II | (5-6) | | | | | | | I | (5-6) |
| *Rhododendron ponticum* | II | (1-2) | | | | | | | I | (1-2) |
| *Plagiochila spinulosa* | II | | | | | | | | I | |
| | | | | | | | | | | |
| **Group 2** | | | | | | | | | | |
| | | | | | | | | | | |
| **Preferential Species** | | | | | | | | | | |
| *Calluna vulgaris* | III | (1-5) | V | (5-8) | III | (4-5) | III | (2) | III | (1-8) |
| *Dicranum scoparium* | IV | | V | | III | | II | | III | |
| *Sphagnum palustre* | | | V | | | | II | | I | |
| *Calypogeia fissa* | I | | III | | | | | | I | |
| *Campylopus introflexus* | | | III | | I | | | | I | |
| | | | | | | | | | | |
| **Differential Species** | | | | | | | | | | |
| *Eriophorum vaginatum* | | | V | (4) | | | | | I | (4) |
| *Empetrum nigrum* | | | V | (3) | | | | | I | (3) |
| *Erica tetralix* | | | V | (1-2) | | | | | I | (1-2) |
| *Andromeda polifolia* | | | V | (1) | | | | | I | (1) |
| *Vaccinium oxycoccus* | | | V | (1) | | | | | I | (1) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Phragmites australis* | | | III | (3) | | | | | I | (3) |
| *Dryopteris carthusiana* | | | III | (1) | | | | | I | (1) |
| *Eriophorum angustifolium* | | | III | (1) | | | | | I | (1) |
| *Aulacomnium palustre* | | | III | | | | | | I | |
| *Sphagnum fimbriatum* | | | III | | | | | | I | |
| *Sphagnum magellanicum* | | | III | | | | | | I | |
| *Sphagnum squarrosum* | | | III | | | | | | I | |
| **Group 3** | | | | | | | | | | |
| **Preferential Species** | | | | | | | | | | |
| *Corylus avellana* | I | (2) | | | V | (4-8) | | | II | (2-8) |
| *Anthoxanthum odoratum* | II | (+) | III | (1) | V | (+-4) | II | (7) | III | (+-7) |
| *Lonicera periclymenum* | III | (+-4) | | | V | (+-4) | | | III | (+-4) |
| *Viola riviniana / reichenbachiana* | I | (2) | | | V | (+-2) | II | (1) | II | (+-2) |
| *Rhytidiadelphus triquetrus* | II | | | | V | | III | | III | |
| *Festuca ovina* | I | (1) | | | IV | (1-5) | II | (1) | II | (1-5) |
| *Eurhynchium striatum* | II | | | | IV | | | | II | |
| *Ulota crispa* | I | | | | II | | | | I | |
| **Differential Species** | | | | | | | | | | |
| *Fraxinus excelsior* | | | | | V | (1-6) | | | II | (1-6) |
| *Brachypodium sylvaticum* | | | | | V | (+-7) | | | II | (+-7) |
| *Crataegus monogyna* | | | | | V | (+-6) | | | II | (+-6) |
| *Prunus spinosa* | | | | | IV | (1-4) | | | I | (1-4) |
| *Teucrium scorodonia* | | | | | IV | (1-4) | | | I | (1-4) |
| *Ctenidium molluscum* | | | | | IV | | | | I | |
| *Succisa pratensis* | | | | | III | (1-2) | | | I | (1-2) |
| *Arum maculatum* | | | | | III | (+-3) | | | I | (+-3) |
| *Fragaria vesca* | | | | | III | (+-3) | | | I | (+-3) |
| *Rosa pimpinellifolia* | | | | | III | (+-3) | | | I | (+-3) |
| *Hypericum pulchrum* | | | | | III | (+) | | | I | (+) |
| *Neckera crispa* | | | | | III | | | | I | |
| *Tortella tortuosa* | | | | | III | | | | I | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Sesleria caerulea* | | | | | II | (4-5) | | I | (4-5) |
| *Rubus saxatilis* | | | | | II | (4) | | I | (4) |
| *Geranium sanguineum* | | | | | II | (2-3) | | I | (2-3) |
| *Thymus praecox* | | | | | II | (1-3) | | I | (1-3) |
| *Carex flacca* | | | | | II | (1) | | I | (1) |
| *Geranium robertianum* | | | | | II | (1) | | I | (1) |
| *Veronica chamaedrys* | | | | | II | (1) | | I | (1) |
| *Lotus corniculatus* | | | | | II | (+-2) | | I | (+-2) |
| *Hypochoeris radicata* | | | | | II | (+-1) | | I | (+-1) |
| *Epipactis helleborine* | | | | | II | (+) | | I | (+) |
| *Potentilla sterilis* | | | | | II | (+) | | I | (+) |
| *Taraxacum* agg. | | | | | II | (+) | | I | (+) |
| *Breutelia chrysocoma* | | | | | II | | | I | |
| *Isothecium alopecuroides* | | | | | II | | | I | |

**Group 4**

**Preferential Species**

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Galium saxatile* | I | (1) | | | | V | (+-4) | II | (+-4) |
| *Plagiothecium undulatum* | III | | III | I | | V | | III | |
| *Agrostis capillaris* | II | (1) | | II | (+-5) | IV | (3-4) | II | (+-5) |
| *Oxalis acetosella* | II | (2-4) | | I | (5) | IV | (2-4) | II | (2-5) |
| *Polytrichastrum formosum* | II | | III | I | | IV | | II | |
| *Rhytidiadelphus loreus* | II | | | | | IV | | II | |
| *Molinia caerulea* | II | (1-5) | | I | (5) | III | (4-9) | II | (1-9) |
| *Deschampsia flexuosa* | I | (4) | | I | (1) | III | (4) | I | (1-4) |
| *Agrostis stolonifera* | I | (1) | | II | (3-4) | III | (1-3) | II | (1-4) |
| *Dryopteris aemula* | I | (1) | | | | III | (1) | I | (1) |
| *Mnium hornum* | II | | | | | III | | II | |
| *Rhytidiadelphus squarrosus* | | | | II | | III | | I | |
| *Hymenophyllum wilsonii* | I | (3) | | | | II | (3) | I | (3) |
| *Erica cinerea* | I | (+) | | I | (3) | II | (1) | I | (1) |
| *Trifolium repens* | | | | I | (1) | II | (1) | I | (1) |
| *Dactylis glomerata* | I | (+) | | I | (3) | II | (+) | I | (+-3) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Campylopus flexuosus* | I | | | | | II | | I | |
| **Differential Species** | | | | | | | | | |
| *Agrostis vinealis* | | | | | | II | (4) | I | (4) |
| *Holcus lanatus* | | | | | | II | (4) | I | (4) |
| *Arrhenatherum elatius* | | | | | | II | (1) | I | (1) |
| *Cerastium fontanum* | | | | | | II | (1) | I | (1) |
| *Cirsium palustre* | | | | | | II | (1) | I | (1) |
| *Luzula multiflora* | | | | | | II | (1) | I | (1) |
| *Lysimachia nemorosa* | | | | | | II | (1) | I | (1) |
| *Ranunculus repens* | | | | | | II | (1) | I | (1) |
| *Stellaria holostea* | | | | | | II | (1) | I | (1) |
| *Cardamine* sp. | | | | | | II | (+) | I | (+) |
| *Danthonia decumbens* | | | | | | II | (+) | I | (+) |
| *Festuca rubra* | | | | | | II | (+) | I | (+) |
| *Juncus effusus* | | | | | | II | (+) | I | (+) |
| *Rhizomnium punctatum* | | | | | | II | | I | |
| *Sphagnum quinquefarium* | | | | | | II | | I | |
| *Thamnobryum alopecurum* | | | | | | II | | I | |

| **Summary Data** | | **SE** | | **SE** | | **SE** | | **SE** | | **SE** |
|---|---|---|---|---|---|---|---|---|---|---|
| Mean Species Richness | 14.9 | ± 2.5 | 12.5 | ± 0.5 | 31.2 | ± 5.8 | 17.0 | ± 3.2 | 20.0 | ± 2.6 |
| Mean Altitude (m) | 100.0 | ± 18.9 | 54.5 | ± 9.5 | 45.0 | ± 21.5 | 270.3 | ± 24.7 | 113.0 | ± 21.5 |
| Mean Slope ($^{o}$) | 12.1 | ± 3.8 | 0.0 | ± 0.0 | 7.5 | ± 4.6 | 17.3 | ± 4.2 | 10.6 | ± 2.4 |
| Mean Soil pH | 3.56 | | 3.34 | | 4.46 | | 3.62 | | 3.67 | |
| Mean Soil Organic Content (%) | 63.1 | ± 8.4 | 96.0 | ± 2.6 | 42.2 | ± 10.0 | 53.2 | ± 12.8 | 58.1 | ± 6.0 |
| Mean Density (trees/ha) | 981.3 | ± 202.9 | 912.5 | ± 487.5 | 600 | ± 197.9 | 512.5 | ± 154.6 | 766.3 | ± 115.6 |
| Mean Canopy Height (m) | 16.2 | ± 0.3 | 8.4 | ± 0.2 | 15.5 | ± 0.8 | 13.6 | ± 0.2 | 14.3 | ± 0.3 |

Frequency classes are denoted by Roman numerals as follows: 1-20% = I, 21-40% = II, 41-60% = III, 61-80% = IV, 81-100% = V. Abundance is presented for vascular plants as a bracketed range of Domin values. Species occurring in only one group with a frequency of I have been omitted from the table but are listed below, with the Domin values of vascular plants given in brackets. Group 1: *Betula pendula* (4); *Alnus glutinosa* (3); *Hymenophyllum tunbrigense* (1);

*Euphorbia hyberna*, *Picea sitchensis*, *Saxifraga spathularis* (+); *Calypogeia muelleriana*, *Diplophyllum albicans*, *Hookeria lucens*, *Leucobryum glaucum*. Group 3: *Filipendula ulmaria* (4); *Carex sylvatica*, *Euonymus europaeus*, *Plantago lanceolata*, *Rhamnus cathartica*, *Rosa canina*, *Stellaria media* (3); *Larix decidua*, *Melampyrum pratensis*, *Polystichum setiferum*, *Viburnum opulus* (2); *Angelica sylvestris*, *Ceratocapnos claviculata*, *Daucus carota*, *Festuca arundinacea*, *Galium verum*, *Koeleria macrantha*, *Ranunculus acris*, *Rubia peregrina*, *Salix* x *multinervis*, *Trifolium pratense*, *Umbilicus rupestris* (1); *Acer pseudoplatanus*, *Antennaria dioica*, *Avenula pubescens*, *Campanula rotundifolia*, *Centaurea nigra*, *Cytisus scoparius*, *Epilobium* sp., *Galium aparine*, *Iris pseudacorus*, *Lapsana communis*, *Lathyrus linifolius*, *L. pratensis*, *Lythrum salicaria*, *Mycelis muralis*, *Phleum pratense*, *Polygala vulgaris*, *Rumex acetosella*, *Salix repens*, *Schoenus nigricans*, *Sedum anglicum*, *Senecio jacobaea*, *Valeriana officinalis*, *Veronica officinalis*, *Vicia cracca* (+); *Calliergonella cuspidatum*, *Ditrichum gracile*, *Frullania dilatata*, *Homalothecium sericeum*, *Hypnum lacunosum*, *Lophocolea heterophylla*, *Neckera complanata*, *Plagiomnium undulatum*.

### 4.5.2 Classification of Putative Vegetation Communities

There was broad agreement between the cluster analysis and NMS output, as the hierarchy and natural groups corresponded to reasonably well defined areas on the ordinations. This implies that there is a good basis for describing the natural groups as distinct vegetation types. The groups are generally well defined in terms of the environmental conditions in which they occur, their preferential and differential species and they also make good ecological sense. It is acknowledged that the lack of *p*-values prevents the identification of statistically significant indicator species. However, the definition of vegetation communities must preserve their ecological integrity above the minutiae of mathematical technique (Rodwell, 1991b; van der Maarel, 2007) and the ecological integrity of these groups appears to be satisfactory.

The putative vegetation types defined in this study correspond to recognisable semi-natural vegetation types. Group 1, the *Vaccinium myrtillus-Ilex aquifolium* type appears to represent acid oak woodland with a *P. sylvestris* component. This group is broadly comparable with Fossitt's (2000) oak-birch-holly semi-natural woodland (WN1) category, which is linked to the 'old sessile oak woods with *Ilex* and *Blechnum* in the British Isles' category on Annex I of the EU Habitats Directive (91A0) (EEC, 1992). All of these plots originated as plantations. The presence of *Rhododendron ponticum*, *Picea sitchensis* and *Fagus sylvatica* regeneration within this vegetation type highlights its vulnerability to invasive non-native species. This vegetation type is associated with acidic mor humus soils on sloping ground at moderate altitudes.

Group 2, the *Calluna vulgaris-Eriophorum vaginatum* type, clearly represents Fossitt's (2000) semi-natural bog woodland (WN7) category, which is linked to the bog woodland category on Annex I of the EU Habitats Directive (91D0) (EEC, 1992). This vegetation type is particularly well defined as it contains five perfect

differential species and both sites were located on active raised bogs which exhibited very similar environmental conditions – flat topography and acidic, waterlogged peat soils with a high organic content. The vegetation histories of these sites were investigated using palaeoecological techniques and both were found to be non-relict, naturalised stands (O'Connell & Doyle, 1990; Heery, 1993). The small sample size of this group is due to the rarity of this habitat in Ireland (Fossitt, 2000).

Group 3, the *Corylus avellana-Brachypodium sylvaticum* type, is relatively heterogeneous but appears to represent both naturalised and planted stands with exposed or outcropping rock and/or relatively high soil pH values, which generally occur on gently sloping ground in the lowlands. Most of the differential and preferential species display a preference for soil pH in the range of 5-7 and some such as *Teucrium scorodonia* display a preference for rocky habitats (Grime *et al.*, 1988). Overall, this group corresponds loosely with Fossitt's (2000) semi-natural oak-ash-hazel woodland (WN2) category which, although it is not listed under Annex I of the EU Habitats Directive, is limited in extent in Ireland and should be considered as being of conservation importance. However, due to the heterogeneity of the group, there may be some basis for its sub-division. Figure 4.3 highlights the relative similarity of Plots 3, 13 and 20. These plots represent a complex, small-scale vegetation mosaic which is associated with karstic areas of the Burren in western Ireland (Cross, 1998) and is of particular conservation interest. They correspond with a transitional habitat – dry calcareous and neutral grassland (GS1) grading into scrub (WS1). They also incorporate elements of limestone pavement (ER2) and dry calcareous heath (HH2) (Fossitt, 2000). Most of these are listed habitats under Annex I of the EU Habitats Directive. Calcareous and neutral grassland corresponds to the priority habitat 'semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (important orchid sites)' (6210). Limestone pavement is also a priority habitat (8240). Dry calcareous heath corresponds to 'European dry heaths' (4030) (EEC, 1992). The relatively high $\alpha$ diversity of these plots (Fig. 4.2) contributes to their

relatively high species richness (Fig. 4.5) and heightens their conservation importance.

Group 4, the *Galium saxatile-Agrostis capillaris* type, does not correspond clearly to any one habitat type, but its species composition bears some similarity to that of flushes (PF2), exposed siliceous rock (ER1) and particularly to dry-humid acid grassland (GS3), all habitats which do not typically occur under a woodland canopy (Fossitt, 2000). Rodwell & Cooper (1995) attributed this tendency to the modest shade cast by *P. sylvestris* stands, which means that there are often few differences in species composition, other than the presence of *P. sylvestris* itself, between the woodland and the habitat that the tree has colonised. Appropriately, this group is characterised by an open structure as it exhibits the lowest density of trees (Table 4.3). This vegetation type is associated with acid soils in upland situations and these plots all originated as plantations.

### 4.5.3 Effects of Environmental Factors on Putative Vegetation Communities

Soil pH accounted for the largest proportion of variance in species composition in *P. sylvestris* stands. Soil pH also exhibited a highly significant positive correlation with species richness (Table 4.2), a relationship which has been observed throughout temperate regions of Europe (Partel *et al.*, 2004). Altitude and slope also accounted for large proportions of the variance in species composition, but did not exhibit a significant correlation with species richness. This suggests that soil pH, altitude and slope have a role in partitioning distinct vegetation types and that increasing soil pH positively influences the species diversity of *P. sylvestris* stands.

## 4.6 Conclusions

*P. sylvestris* tolerates a wide range of environmental conditions in the Irish context. Varying levels of soil pH, altitude and slope produce markedly different, but reasonably well defined, vegetation communities. Soil pH may potentially act as an indicator of species diversity for *P. sylvestris* woodland in Ireland. In terms of forest management, the quantitative environmental data presented here should inform site selection for new plantings of *P. sylvestris* and species selection at any given site.

*P. sylvestris* is well established, well integrated and naturalising in Irish semi-natural habitats. Its associated vegetation communities are diverse. A low level of species constancy and a high level of β diversity reflect this diversity and variability. These communities contain a high proportion of native species. Furthermore, the comparison of these communities with those described in Fossitt (2000) has shown that, excepting the presence of a questionably native species in the canopy, these habitats exhibit a semi-natural character. Given Ireland's impoverished native flora and low coverage of native woodland, these communities form a significant resource for native biodiversity. In addition, some of the communities described here correspond to habitats of international conservation importance. Woodlands of intact raised bog, in particular, are acknowledged as being very rare in Ireland (Cross, 1987; Fossitt, 2000). Whether or not *P. sylvestris* is native, the communities associated with it in Ireland are of value in conserving Ireland's native botanical and habitat diversity. The baseline vegetation data presented here should inform conservation policy relating to *P. sylvestris* in Ireland, and are broadly relevant in assessing the conservation value of reintroduced species elsewhere.

Future work will include a formal comparison of these Irish sites with native pinewoods in Scotland, thereby placing Irish pinewoods in the broader context of the flora of north-west Europe.

# 5. Vegetation ecology of *Pinus sylvestris* forests in oceanic north-west Europe: a comparison of reintroduced and native stands

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Plate 5.1. Photograph of the pinewood canopy at Abernethy in the Scottish Highlands.

## 5.1 Abstract

*Pinus sylvestris* underwent extirpation and reintroduction in some north-west European countries and its native status there is now unclear. Information on the ecological implications of this reintroduction is needed to inform conservation and forest management strategies. This paper aims to test the hypothesis that the vegetation of reintroduced *P. sylvestris* forests is similar to that of their native counterparts, using case studies in oceanic north-west Europe.

In order to assess their conservation value and place them within the European context, 20 plots from reintroduced Irish pinewoods were compared with seven plots from native Scottish pinewoods of high biological quality. Floristic and environmental data were analysed using non-parametric and multivariate statistical techniques and a synoptic table was prepared. Qualitative comparisons were made with native pinewoods in continental Europe, with emphasis on oceanic western Norway.

Cluster analysis produced four reasonably well defined groups, two of which demonstrated a direct correspondence between reintroduced Irish and native Scottish pinewoods. The Irish *Calluna vulgaris-Eriophorum vaginatum* bog woodland type corresponded closely with the Scottish *P. sylvestris*-dominated bog woodland type, a habitat of international conservation importance. The Irish *Galium saxatile-Agrostis capillaris* type corresponded with a putative *Molinia caerulea*-dominated sub-community of the typical Caledonian forest vegetation type. Although the other groups did not correspond directly to the Scottish plots they were qualitatively linked to continental European native pine forest types. The Irish *Vaccinium myrtillus-Ilex aquifolium* and *Corylus avellana-Brachypodium sylvaticum* types were linked to the *Querco-Pinetum* association and the Fennoscandian *Convallario-Pinetum* association respectively.

Reintroduced pinewoods are an important resource for Ireland's native botanical and habitat diversity. They behave, to a greater or lesser extent, like native ecosystems in the nearest regions where such forests occur. In particular, the *Calluna vulgaris-Eriophorum vaginatum* bog woodland type is of conservation importance. For practical conservation purposes, *P. sylvestris* should be managed as a native species in Irish woodlands despite its reintroduced status.

## 5.2 Introduction

The native forests of Europe have either been modified by centuries of management or are secondary formations on land which was previously cleared. Few, if any, examples of virgin forest remain, at least in north-west Europe (Peterken, 1996). The debate regarding the role of plantation forests in the maintenance and enhancement of biodiversity (Hartley, 2002; Stephens & Wagner, 2007; Brockerhoff *et al.*, 2008) takes on particular significance in countries where the area of plantations is high relative to that of semi-natural forest. In Belgium, Denmark and the UK, for example, plantations constitute 41.0, 63.0 and 67.6% of forest cover respectively. In Ireland, a very low proportion (9.7%) of the land area is forested and a very high proportion of this (86.5%) consists of plantations (FAO, 2007). Where semi-natural forests are so scarce, and particularly where sustainable forest management is applied, non-native plantations assume importance as a resource for biodiversity (Brockerhoff *et al.*, 2008).

Ireland's island status, small size and low coverage of native woodland makes it a useful model study side for examining the contribution that non-native, or questionably native, tree species can make to the conservation of native biodiversity. Due to its glacial history, location at the edge of Europe and, again, its small size and island status, Ireland's native botanical diversity is significantly lower than elsewhere in north-west Europe, with a vascular flora of just 815

species, excluding Pteridophytes and apomictic microspecies (Webb, 1983). Substantial research has been conducted on the vegetation ecology of both native forests (Perrin *et al.*, 2006; Perrin *et al.*, 2008b) and non-native plantations (Iremonger *et al.*, 2006; French *et al.*, 2008) in Ireland but the ecology of *P. sylvestris*, a reintroduced species, has been largely overlooked until recently (Roche *et al.*, 2009).

Palaeoecological evidence indicates that *P. sylvestris* colonised Ireland by 9500 BP (radiocarbon years before present) (Mitchell, 2006), becoming an important component of certain habitats until a major decline began about 4000 BP (Bradshaw & Browne, 1987). The species is believed to have been extirpated around 1600 BP (McAulay & Watts, 1961) but had been reintroduced by the eighteenth century (Pococke, 1891) and has since been widely planted. This sequence of extirpation and reintroduction is also thought to have occurred in several other north-west European countries, namely Belgium, Denmark, the Netherlands, England and Wales (Mirov, 1967; Jalas & Suominen, 1973; Bennett, 1984; Bradshaw, 1993; Le Maitre, 1998; Lust *et al.*, 2000). Interestingly, these regions roughly coincide with the highest proportions of plantation forests in Europe (FAO, 2007) and a clear absence of virgin forest (Peterken, 1996). These are the conditions under which non-native plantations assume importance as a resource for native biodiversity, but what contribution can be made by a reintroduced species?

The native/alien paradigm, which underlies many conservation and management policies (Warren, 2007), is blurred in the case of *P. sylvestris*. As a result of its extirpation and reintroduction, its native status in Ireland is disputed and the relevant conservation and forest management strategies are often disjointed. For example, the Irish Native Woodland Scheme provides financial incentives for the planting of *P. sylvestris* in semi-natural habitats (Forest Service, 2001), whereas the Irish Peatland Conservation Council lists it as an invasive non-native species (Malone & O'Connell, 2009). Clarification is therefore urgently required on the

implications of this reintroduction for the conservation of native biodiversity. The vegetation of Irish pinewoods was recently described (Roche *et al.*, 2009), providing necessary baseline information but also raising further questions about the classification and conservation value of these communities. Webb (1983) stated that to understand the ecology of a plant species in Ireland, the chosen species must also be studied abroad. The next step in defining Irish pinewoods in a broader geographical context is therefore to examine native pine forests in the nearest regions where such forests occur.

Scotland and western Norway provide valid reference points for this comparison. Within the British Isles, native pinewoods are restricted to the Scottish Highlands (Steven & Carlisle, 1959). Caledonian forest and bog woodland are priority habitats under Annex I of the European Union Habitats Directive (NATURA 2000 codes 91C0 and 91D0 respectively) (EEC, 1992) and are therefore recognised as being of international conservation importance. Comprehensive national and regional plans for the protection of conifer forests have been developed in Norway, Sweden and Finland. Important pine forest types have been designated as nature reserves and key biotope protection areas and old-growth stands in northern Fennoscandia form important elements in National Parks. Several accounts of the vegetation of both Scottish and Fennoscandian pinewoods have been published (Steven & Carlisle, 1959; McVean & Ratcliffe, 1962; Kielland-Lund, 1967; Sjörs, 1967; Birse, 1980; Kielland-Lund, 1981; Rodwell, 1991b; Påhlsson, 1994; Fremstad, 1997). Climatic conditions are broadly comparable within the study area, being oceanic throughout, although it should be noted that Scotland becomes more boreal towards the east. There is also a pronounced oceanic-continental gradient from the coast to the interior fjord and valley districts in western Norway, which is reflected in the floristic composition of the pine forests.

This paper aims to test the hypothesis that the vegetation composition of reintroduced *P. sylvestris* forests is similar to that of their native counterparts,

using case studies in oceanic north-west Europe. Quantitative comparisons are made between the vegetation of reintroduced pinewoods in Ireland and native pinewoods of high biological quality in Scotland. Detailed qualitative comparisons are made with native pinewoods in western Norway and more general parallels are drawn with those elsewhere in continental Europe. This comparison will provide an indication of the conservation value of reintroduced stands and place the recently described Irish pinewoods within the European phytosociological framework.

## 5.3 Methods

### 5.3.1 Quantitative Comparison – Site Selection

The criteria used in the selection of 18 Irish sites are described in Roche *et al.* (2009). Planted and naturalised stands and those of unknown origin were included. The selection of six Scottish sites was informed by vegetation descriptions (Steven & Carlisle, 1959; McVean, 1963; Birse, 1980; Rodwell, 1991b), the Caledonian Pinewood Inventory (Forestry Commission, 1998) and descriptions of designated sites (McLeod *et al.*, 2005). To ensure their high biological quality, survey sites were selected from the list of Special Areas of Conservation (SACs) designated for grade A or B Caledonian forest and/or bog woodland (McLeod *et al.*, 2005), where *P. sylvestris* is known to be native (Steven & Carlisle, 1959). One exception was Glen Loy, which is designated as a Site of Special Scientific Interest and was selected to represent a particular genetic mitotype of *P. sylvestris* (Sinclair *et al.*, 1998). To foster comparability between Irish and Scottish sites, northern- and easternmost Scotland were excluded and sites were selected within the same altitudinal range. The sites and their locations are shown in Table 5.1 and Figure 5.1.

Table 5.1. Location of the 27 survey plots shown in Figure 5.1.

| Plot Number | Plot Name | County/Region | Country | Irish/UK Grid References |
|---|---|---|---|---|
| I1 | Dale Wood | Kerry | Ireland | V 88181 80714 |
| I2 | Clonfinane Bog | Tipperary | Ireland | M 98815 03715 |
| I3 | Rockforest | Clare | Ireland | R 34755 95013 |
| I4 | Priest's Leap | Cork | Ireland | V 98853 59132 |
| I5 | Glengarriff | Cork | Ireland | V 90894 56831 |
| I6 | All Saints Bog | Offaly | Ireland | N 01203 11216 |
| I7 | Glenfarne | Leitrim | Ireland | H 02059 39747 |
| I8 | The Scalp | Dublin | Ireland | O 21719 20093 |
| I9 | Coronation Plantation | Wicklow | Ireland | O 09708 12792 |
| I10 | Derrycrag - Plot 1 | Galway | Ireland | R 73616 99077 |
| I11 | Derrycrag - Plot 2 | Galway | Ireland | R 73652 99029 |
| I12 | Portumna Forest Park | Galway | Ireland | M 82680 03320 |
| I13 | Rockvale | Clare | Ireland | R 38955 98090 |
| I14 | Torc | Kerry | Ireland | V 96482 83719 |
| I15 | Knockastakeen | Tipperary | Ireland | R 93807 27204 |
| I16 | Trooperstown | Wicklow | Ireland | T 15932 96721 |
| I17 | Derrybawn | Wicklow | Ireland | T 12365 96360 |
| I18 | Vale of Clara | Wicklow | Ireland | T 17212 92127 |
| I19 | Ballykine - Plot 1 | Mayo | Ireland | M 10849 57328 |
| I20 | Ballykine - Plot 2 | Mayo | Ireland | M 10657 57113 |
| S21 | Cona Glen | Highland | Scotland | NM 97238 71210 |
| S22 | Glen Loy | Highland | Scotland | NN 09495 84288 |
| S23 | Glen Affric | Highland | Scotland | NH 19283 22800 |
| S24 | Beinn Eighe | Highland | Scotland | NH 00351 64685 |
| S25 | Abernethy - Plot 1 | Highland | Scotland | NH 96226 17443 |
| S26 | Abernethy - Plot 2 | Highland | Scotland | NH 97612 17191 |
| S27 | Black Wood of Rannoch | Perth and Kinross | Scotland | NN 56968 56176 |

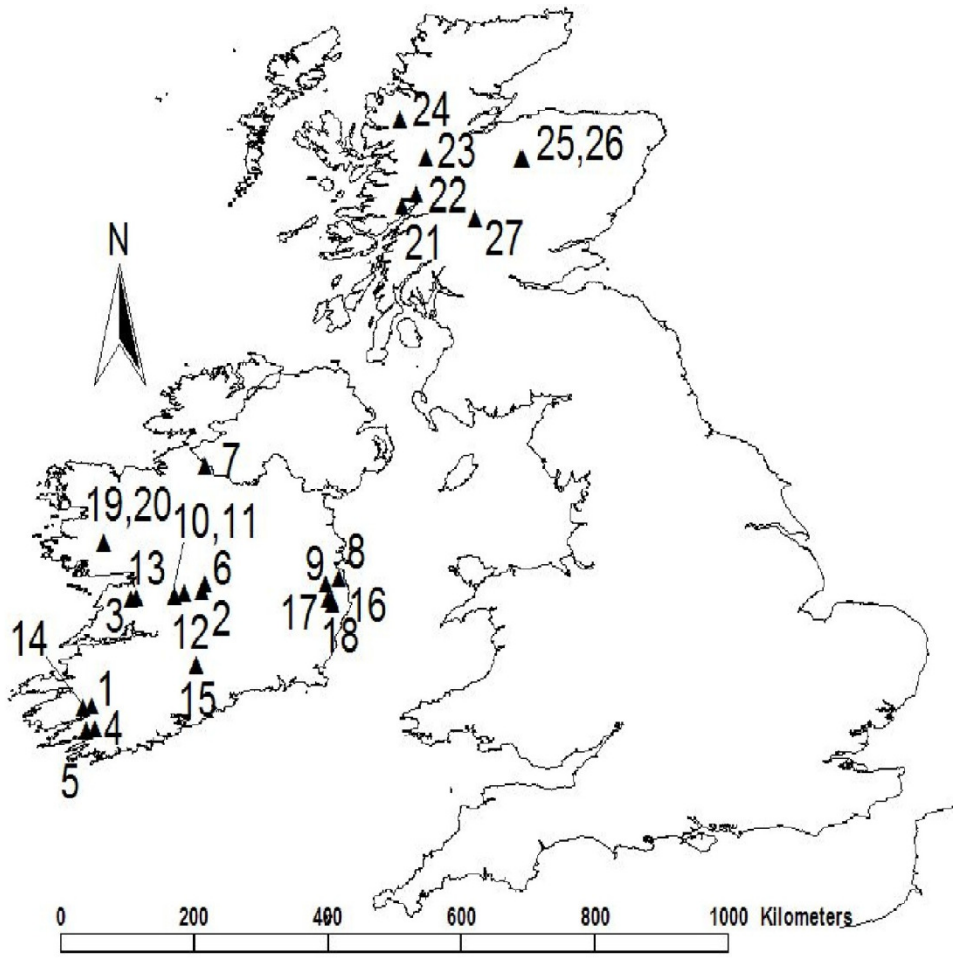



Figure 5.1. Location map of the 27 survey plots in Ireland and Scotland, listed in Table 5.1.

### 5.3.2 Data Collection

Field surveys were conducted from May - September 2006 and April - August 2007. We surveyed 27 plots at 24 sites (Table 5.1, Fig. 5.1), as two apparently different *P. sylvestris*-dominated vegetation types occurred at each of the Derrycrag, Ballykine and Abernethy sites. As illustrated in Roche *et al.* (2008, Appendix 4.1), a circular 400 $m^2$ plot was subjectively placed to represent each *P. sylvestris* vegetation type. This shape was selected to facilitate a study of pollen

dispersal which is not presented here. Five 2 x 2 $m^2$ quadrats were placed within this plot, one at the centre and at each of the cardinal points. This quadrat size was chosen to capture ground flora diversity, where the dominant structural form varied from herbs to sub-shrubs. In each of these quadrats, floristic data were recorded on the Domin scale (Dahl & Hadac, 1941) for woody species and herbs. Nomenclature followed Stace (1997). The slope, altitude and national grid coordinates of the plot were recorded. In each quadrat, five 10 cm deep soil samples were taken and bulked in the field. Soil pH was determined in the laboratory using a WTW pH 330 meter and combination electrode. Soil % organic content was determined by loss on ignition at 550$^o$ C using a Thermolyne Type 6000 furnace. Approximate soil bulk density was estimated from % organic content (Jeffrey, 1970).

### 5.3.3 Data Analysis

The nested sampling design involved five 4 $m^2$ quadrats within each plot. As described in Roche *et al.* (2009), the Domin cover values were transformed to estimates of percentage cover, following Currall's (1987) method. A mean of the resulting values was calculated, providing summary data at the scale of the 400 $m^2$ plot. The mean values were reconverted to the Domin scale. This format was thought to be the most defensible option given the sampling design used, but was incompatible with certain data analysis techniques such as Indicator Species Analysis (Podani, 2006).

Data screening, transformation and multivariate analyses were carried out using PC-ORD 5 (McCune & Mefford, 2005). Data were screened by Outlier Analysis. No species were identified as outliers. Plot I12 was identified as an outlier (sd = 2.17), probably due to an unusually high abundance of *Brachypodium sylvaticum*, and was excluded from the dataset to prevent undue influence on the results. Rare species, i.e. those present in only one plot (3.8%), were deleted to reduce noise in

the dataset (McCune & Grace, 2002). A hierarchical, agglomerative, polythetic method of Cluster Analysis was used for classification. Sørensen's (Bray-Curtis) distance measure was used with the Flexible Beta linkage method, with parameter β set at -0.25 (Lance & Williams, 1967). Nonmetric Multidimensional Scaling (NMS) was used for ordination and was run from a random starting configuration in slow and thorough autopilot mode with Sørensen set as the distance measure. The stability criterion was set at 0.00001 and the number of iterations to evaluate stability was set at 15. A Monte Carlo test was carried out with 250 randomized runs. The similarity of plots was assessed by the identification of groups on the cluster dendrogram and verified with reference to the structure of the NMS ordination. The non-parametric Spearman's rank correlation coefficient was calculated for environmental variables, species richness and ordination scores using SPSS 14.0 (SPSS, 2005).

In order to describe the species composition of the groups identified by cluster analysis, floristic data were sorted in a synoptic table in the style of the British National Vegetation Classification (NVC) (Rodwell, 1991b). Rare species, i.e. those present in only one plot, were omitted. Frequency and abundance values for each species, within each group and overall, are presented. Frequency classes are denoted by Roman numerals as follows: 1-20% = I, 21-40% = II, 41-60% = III, 61-80% = IV, 81-100% = V. The terminology used also followed Rodwell (1991b). Constant species are those with an overall frequency of IV or V. General associates are species with an overall frequency of III or less that do not show a marked affiliation to any particular group. Preferential species are distinctly more frequent within one or more of the groups than the others and differential species are those whose affiliation is exclusive to one group.

### 5.3.4 Qualitative Comparison with Norwegian Pine Forests

A review of the literature on Norwegian pinewoods was conducted. The results, informed by JEB's long field experience with Fennoscandian vegetation, were used to produce a classification scheme for the major Nordic pine forest communities, showing the influence of moisture and nutrient gradients (Table 5.4). The Irish pine forest vegetation types were then qualitatively compared with those of western Norway.

## 5.4 Results

### 5.4.1 Multivariate Analysis

The Irish and Scottish dataset contained a total of 132 vascular plant species. The deletion of rare species removed 67 species, or 50.8% of the total. Cluster Analysis produced four reasonably well defined groups (Fig. 5.2). Groups 1 and 3 contained Irish plots only. Group 2 contained two Irish and six Scottish plots. Group 4 contained five Irish and one Scottish plot. NMS found a three-dimensional solution with a final stress of 11.8%, indicating an intermediate solution according to Kruskal's rule of thumb (McCune & Grace, 2002). A Monte Carlo test showed that the probability of a similar final stress being obtained by chance was 0.0040. The groups identified by cluster analysis corresponded to reasonably well defined areas on the NMS ordinations (Fig. 5.3). Group 1 was characterised by low values on Axis 1. It showed some overlap in ordination space with Group 4 (Fig. 5.3a). Group 2 was defined by low values on Axis 2 and also showed some overlap with Group 4 (Fig. 5.3c). Certain distinctions were evident within this group. Cluster analysis (Fig. 5.2) identified two stable sub-groups, which were recognisable by their long stems in the dendrogram (McCune & Grace, 2002). These sub-groups were also apparent in the NMS ordination (Fig. 5.3a), where a tight cluster of plots (S22-S25 and S27) formed about halfway up Axis 3 while a more diffuse 'tail' of plots (S26, I6 and I2, in that order) formed at progressively lower values on Axis 3. Group 3 was characterised by high values

on Axis 1 and was well separated in ordination space (Fig. 5.3b). Group 4 was defined by relatively high values on Axis 3. It was not as well separated, overlapping with Groups 1 and 2 (Fig. 5.3 a, b).

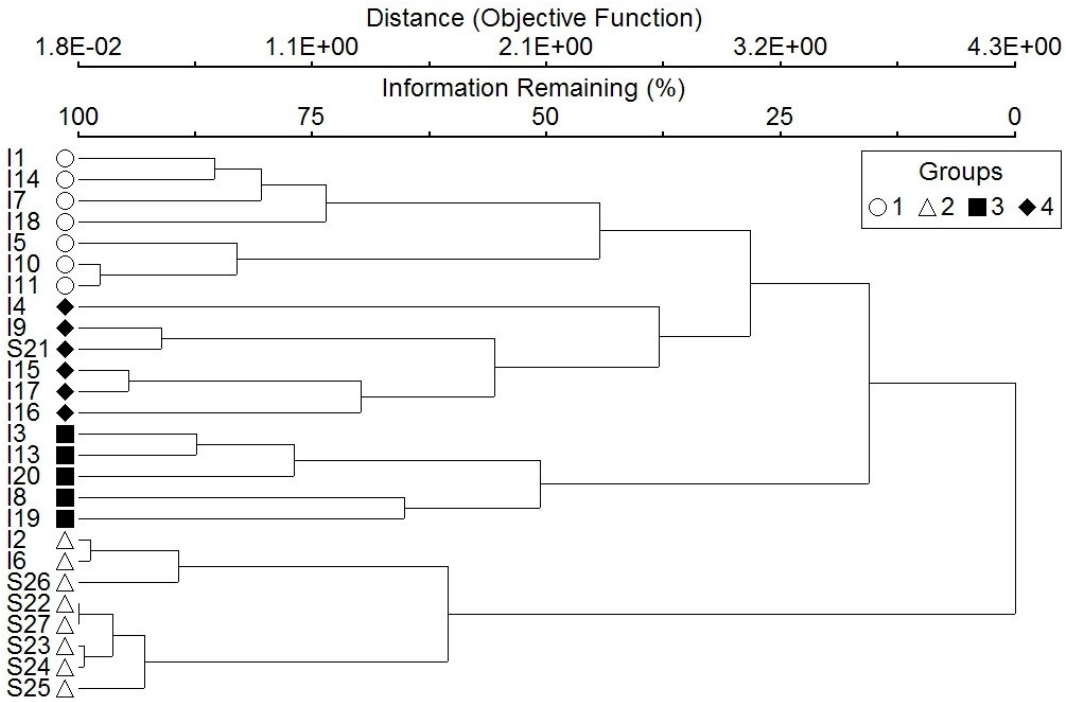



Figure 5.2. Cluster dendrogram of plots listed in Table 5.1, labelled with four groups.

Axis 2 represented the largest proportion of variance in the data ($r^2 = 0.446$) and exhibited extremely significant positive correlations with species richness (r = 0.795) and rock/gravel cover (r = 0.700) (Table 5.2). It separated Groups 2 and 3, so that Group 2 was defined by low species richness and rock/gravel cover and Group 3 by high species richness and rock/gravel cover. Axis 3 represented the second largest proportion of variance in the data ($r^2 = 0.253$) and exhibited extremely significant positive correlations with altitude (r = 0.675) and slope (r = 0.670). This axis separated Group 4, so that it was defined by high altitude and sloping conditions. Axis 1 represented the smallest proportion of variance in the data ($r^2 = 0.133$) and exhibited a highly significant negative correlation with plant

litter cover (r = -0.545). This Axis separated Group 1, so that it was defined by high plant litter cover. Species richness exhibited highly significant positive correlations with coverage of rock/gravel (r = 0.647) and Axis 2 of the NMS ordination (r = 0.795) (Table 5.2). Accordingly Group 2, which was defined by low values on Axis 2, exhibited the lowest species richness overall and Group 3, which was defined by high values on Axis 2, exhibited the highest species richness overall (Table 5.3).

(a)

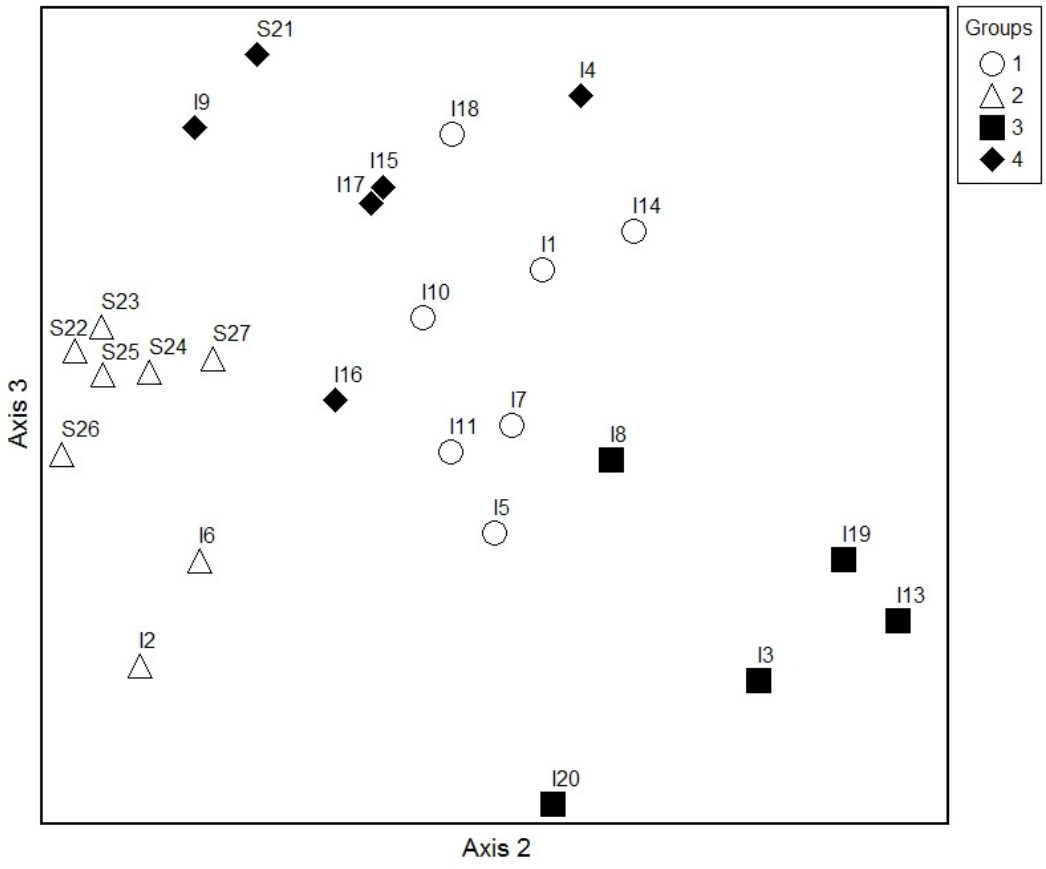
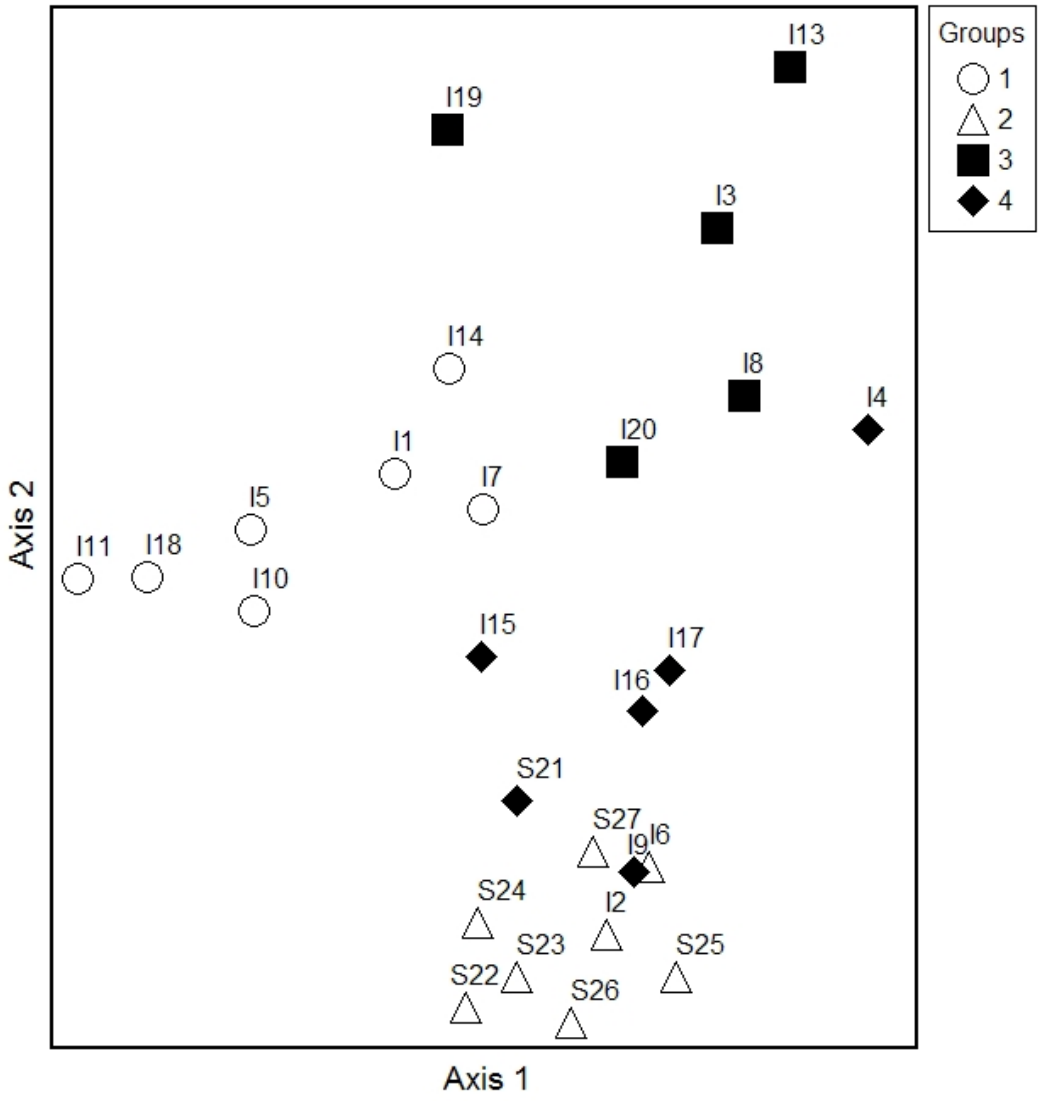



Figure 5.3 (a-c). Nonmetric Multidimensional Scaling ordinations of plots listed in Table 5.1, showing the four groups derived by cluster analysis ($r^2$ values of axes: 1 = 0.133, 2 = 0.446, 3 = 0.253, Total = 0.832). (a) Axes 2 and 3 ($r^2$ = 0.699), (b) Axes 1 and 2 ($r^2$ = 0.579) and (c) Axes 1 and 3 ($r^2$ = 0.386).

(b)


Groups
1
2
3
4
I13
I19
I3
I14
I8
I4
I20
I1
I7
I5
I11
I18
I10
I15
I17
I16
S21
S27
I9
I6
S24
I2
S23
S25
S22
S26
Axis 2
Axis 1

(c)

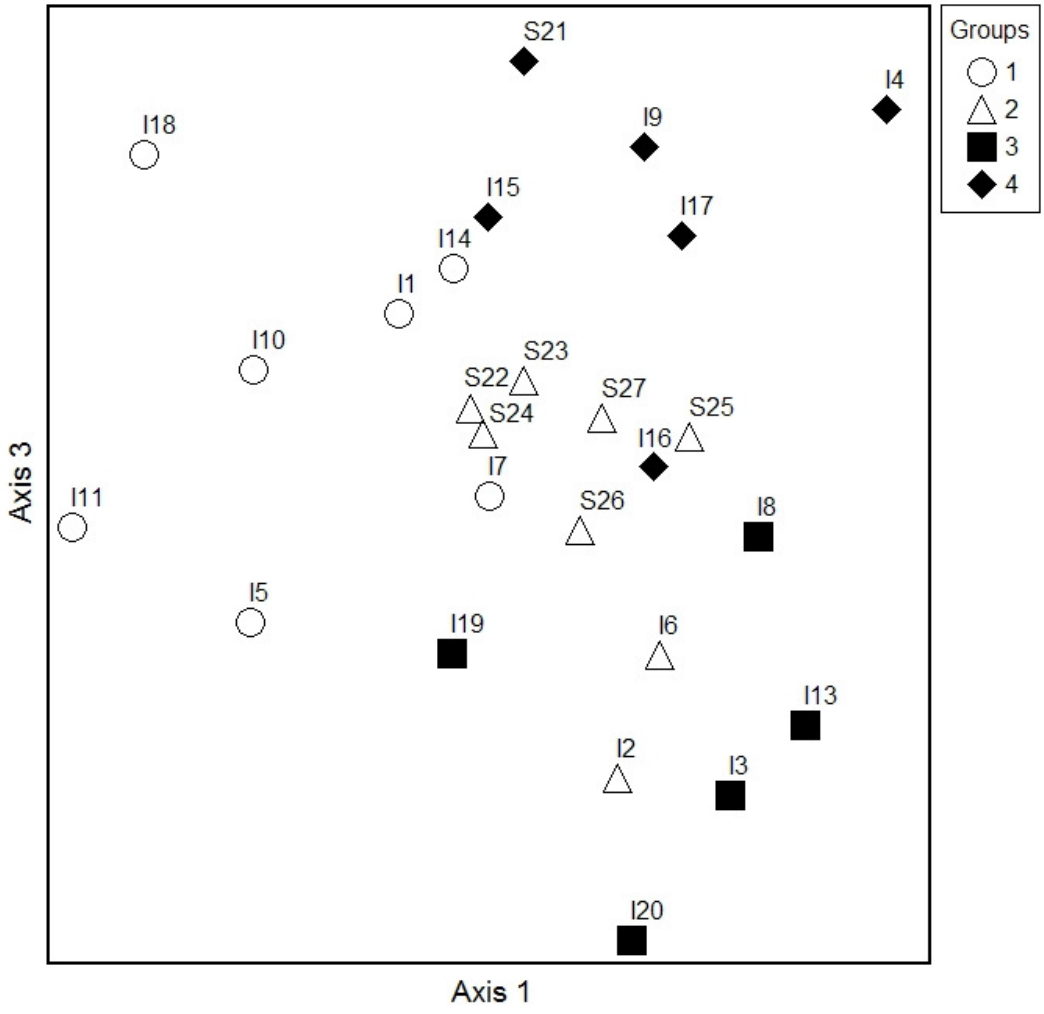

Groups
1
2
3
4
S21
I4
I18
I9
I15
I17
I14
I1
I10
S23
S22
S27
S24
S25
I16
I7
I11
S26
I8
I5
I19
I6
I13
I2
I3
I20
Axis 3
Axis 1

Table 5.2. Spearman rank correlation coefficients for ordination scores, environmental variables and species richness.

| | Axis 1 | Axis 2 | Axis 3 | Soil pH | LOI | Slope | Altitude | Litter | Bare Soil | Rock |
|---|---|---|---|---|---|---|---|---|---|---|
| Soil pH | 0.151 | 0.318 | -0.084 | - | | | | | | |
| LOI | -0.130 | -0.434* | -0.182 | -0.320 | - | | | | | |
| Slope | -0.235 | 0.166 | 0.670*** | 0.157 | -0.316 | - | | | | |
| Altitude | 0.176 | -0.448* | 0.675*** | -0.241 | -0.142 | 0.403* | - | | | |
| Litter | -0.545** | 0.109 | 0.149 | -0.374 | -0.031 | 0.259 | -0.170 | - | | |
| Bare Soil | 0.286 | 0.416* | 0.152 | -0.094 | -0.253 | 0.333 | 0.251 | -0.054 | - | |
| Rock | 0.338 | 0.700*** | -0.110 | 0.276 | -0.401* | 0.323 | -0.085 | -0.011 | 0.607** | - |
| Species Richness | 0.389 | 0.795*** | -0.256 | 0.387 | -0.204 | 0.072 | -0.391 | -0.100 | 0.342 | 0.647** |

Statistically significant correlations are indicated: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

### 5.4.2 Synoptic Table

The constant species, general associates, preferential and differential species and mean species richness for each group are given in Table 5.3.

*Group 1*

Sites: Dale Wood (I1), Glengarriff (I5), Glenfarne (I7), Derrycrag Plot 1 (I10), Derrycrag Plot 2 (I11), Torc (I14), Vale of Clara (I18), N = 7

This group consisted entirely of Irish plots. Its mean species richness was intermediate but comparable with that of Group 4. The invasive, non-native *Rhododendron ponticum* was the only differential species (Table 5.3).

*Group 2*

Sites: Clonfinane Bog (I2), All Saints Bog (I6), Glen Loy (S22), Glen Affric (S23), Beinn Eighe (S24), Abernethy - Plot 1 (S25), Abernethy - Plot 2 (S26), Black Wood of Rannoch (S27), N = 8

This group contained two Irish and six Scottish plots. It had the lowest mean vascular plant species richness overall, being markedly less diverse than the other groups. All of its preferential species were also differential species i.e. they exhibited an exclusive affiliation with this group (Table 5.3).

*Group 3*

Sites: Rockforest (I3), The Scalp (I8), Rockvale (I13), Ballykine Plot 1 (I19), Ballykine Plot 2 (I20), N = 5

This group consisted entirely of Irish plots. It exhibited the highest mean species richness, being markedly more diverse than the other groups (Table 5.3).

*Group 4*

Sites: Priest's Leap (I4), Coronation Plantation (I9), Knockastakeen (I15), Trooperstown (I16), Derrybawn (I17), Cona Glen (S21), N = 6

Group 4 contained five Irish and one Scottish plot. Its mean species richness was intermediate, but comparable with that of Group 1. It had no differential species, as no species exhibited an exclusive affiliation (Table 5.3).

Table 5.3. Synoptic table of floristic data for the four groups derived by cluster analysis.

| **Groups** | **1** | | **2** | | **3** | | **4** | | **Overall** | |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of Plots | 7 | | 8 | | 5 | | 6 | | 26 | |
| Mean Species Richness | 15 | | 9 | | 34 | | 16 | | 17 | |
| **Constant Species** | | | | | | | | | | |
| *Pinus sylvestris* | V | (5-8) | V | (6-8) | V | (4-7) | V | (7-8) | V | (4-8) |
| *Vaccinium myrtillus* | V | (1-7) | V | (2-8) | | | V | (4-8) | IV | (1-8) |
| *Calluna vulgaris* | III | (1-3) | V | (5-8) | III | (4-5) | IV | (+-5) | IV | (+-8) |
| *Pteridium aquilinum* | IV | (+-5) | II | (1-6) | III | (3-5) | V | (+-7) | IV | (+-7) |
| *Sorbus aucuparia* | V | (1-5) | III | (+-3) | II | (1-2) | V | (+-5) | IV | (+-5) |
| **General Associates** | | | | | | | | | | |
| *Blechnum spicant* | V | (+-4) | I | (1) | | | V | (+-3) | III | (+-4) |
| *Oxalis acetosella* | III | (2-4) | | | I | (5) | III | (2-4) | II | (2-5) |
| *Deschampsia flexuosa* | | | III | (+-3) | I | (1) | III | (4) | II | (+-4) |
| *Quercus* hybrids | I | (5) | | | | | I | (6) | I | (5-6) |
| *Hymenophyllum wilsonii* | I | (3) | | | | | I | (3) | I | (3) |
| *Quercus robur* | II | (3-4) | | | II | (1-5) | | | I | (1-5) |
| *Fagus sylvatica* | I | (3) | | | I | (1) | | | I | (1-3) |
| *Agrostis canina* | I | (1) | | | II | (+) | II | (1-3) | I | (+-3) |
| *Dactylis glomerata* | I | (+) | | | I | (3) | I | (+) | I | (+-3) |
| *Erica cinerea* | I | (+) | I | (1) | I | (3) | I | (1) | I | (+-3) |
| *Melampyrum pratense* | | | I | (+) | I | (2) | | | I | (+-2) |
| *Trifolium repens* | | | | | I | (1) | I | (1) | I | (1) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Group 1** | | | | | | | | | | |
| **Preferential Species** | | | | | | | | | | |
| *Ilex aquifolium* | V | (1-8) | | | III | (1-5) | II | (1-2) | III | (1-8) |
| *Quercus petraea* | V | (+-6) | | | I | (4) | | | II | (+-6) |
| *Betula pubescens* | V | (+-5) | II | (5-6) | I | (5) | II | (+-4) | III | (+-6) |
| *Luzula sylvatica* | III | (3-7) | | | | | II | (+-1) | II | (+-7) |
| *Polypodium vulgare* | III | (+-1) | | | II | (+-1) | | | I | (+-1) |
| *Dryopteris dilatata* | II | (1-3) | | | I | (4) | | | I | (1-4) |
| **Differential Species** | | | | | | | | | | |
| *Rhododendron ponticum* | III | (+-2) | | | | | | | I | (+-2) |
| **Group 2** | | | | | | | | | | |
| **Differential Species** | | | | | | | | | | |
| *Vaccinium vitis-idaea* | | | IV | (1-6) | | | | | II | (1-6) |
| *Erica tetralix* | | | IV | (+-4) | | | | | I | (+-4) |
| *Empetrum nigrum* | | | IV | (+-3) | | | | | I | (+-3) |
| *Eriophorum vaginatum* | | | II | (4-6) | | | | | I | (4-6) |
| *Andromeda polifolia* | | | II | (1) | | | | | I | (1) |
| *Vaccinium oxycoccus* | | | II | (1) | | | | | I | (1) |
| **Group 3** | | | | | | | | | | |
| **Preferential Species** | | | | | | | | | | |
| *Corylus avellana* | I | (2) | | | V | (4-8) | | | II | (2-8) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Hedera helix* | III | (+-4) | I | (+) | V | (3-5) | III | (+) | III | (+-5) |
| *Lonicera periclymenum* | III | (+-4) | | | V | (1-4) | I | (1) | II | (+-4) |
| *Rubus fruticosus* agg. | III | (+-4) | II | (+-1) | V | (1-4) | I | (1) | III | (+-4) |
| *Festuca ovina* | I | (1) | I | (+) | IV | (1-5) | II | (+-4) | II | (+-5) |
| *Crataegus monogyna* | | | | | IV | (+-5) | I | (+) | I | (+-5) |
| *Anthoxanthum odoratum* | I | (+) | I | (1) | IV | (+-2) | II | (1-7) | II | (+-7) |
| *Viola riviniana / reichenbachiana* | I | (2) | | | IV | (+-1) | II | (+-1) | II | (+-2) |
| **Differential Species** | | | | | | | | | | |
| *Fraxinus excelsior* | | | | | IV | (2-6) | | | I | (2-6) |
| *Teucrium scorodonia* | | | | | IV | (1-4) | | | I | (1-4) |
| *Brachypodim sylvaticum* | | | | | IV | (+-4) | | | I | (+-4) |
| *Prunus spinosa* | | | | | III | (2-4) | | | I | (2-4) |
| *Fragaria vesca* | | | | | III | (+-3) | | | I | (+-3) |
| *Rosa pimpinellifolia* | | | | | III | (+-3) | | | I | (+-3) |
| *Succisa pratensis* | | | | | III | (+-2) | | | I | (+-2) |
| *Sesleria caerulea* | | | | | II | (4-5) | | | I | (4-5) |
| *Rubus saxatilis* | | | | | II | (4) | | | I | (4) |
| *Geranium sanguineum* | | | | | II | (2-3) | | | I | (2-3) |
| *Geranium robertianum* | | | | | II | (1) | | | I | (1) |
| *Carex flacca* | | | | | II | (1) | | | I | (1) |
| *Thymus polytrichus* | | | | | II | (+-3) | | | I | (+-3) |
| *Lotus corniculatus* | | | | | II | (+-2) | | | I | (+-2) |
| *Hypochoeris radicata* | | | | | II | (+-1) | | | I | (+-1) |
| *Potentilla sterilis* | | | | | II | (+-1) | | | I | (+-1) |
| *Arum maculatum* | | | | | II | (+) | | | I | (+) |
| *Epipactis helleborine* | | | | | II | (+) | | | I | (+) |
| *Hypericum pulchrum* | | | | | II | (+) | | | I | (+) |
| *Taraxacum* agg. | | | | | II | (+) | | | I | (+) |

**Group 4**

**Preferential Species**

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Galium saxatile* | I | (+) | | | | | V | (+-4) | II | (+-4) |
| *Molinia caerulea* | II | (1-5) | II | (1-3) | I | (5) | III | (4-9) | II | (1-9) |
| *Agrostis capillaris* | II | (1) | | | II | (+-5) | III | (3-4) | II | (+-5) |
| *Potentilla erecta* | II | (+-1) | I | (+) | II | (1) | III | (1-3) | II | (+-3) |
| *Betula pendula* | | | I | (5) | | | II | (3-4) | I | (3-5) |
| *Agrostis stolonifera* | I | (1) | | | I | (3) | II | (1-3) | I | (1-3) |
| *Dryopteris aemula* | I | (1) | | | | | II | (1) | I | (1) |

Frequency classes are denoted by Roman numerals as follows: 1-20% = I, 21-40% = II, 41-60% = III, 61-80% = IV, 81-100% = V. Abundance is presented as a bracketed range of Domin values.

## 5.5 Discussion

Group 1 consisted entirely of Irish plots which had all previously been classified as *Vaccinium myrtillus-Ilex aquifolium*, an acid mixed pine-oak woodland type (Roche *et al.*, 2009). The high plant litter coverage associated with this group was probably due to the relative abundance of deciduous broadleaved species, primarily *Quercus petraea* and *Betula pubescens*. The presence of *Rhododendron ponticum* as a differential species reflected the abundance of this non-native invasive in woodlands on acidic, well drained soils in Ireland (Cross, 1982). A slight overlap with Group 4 in the NMS ordination suggested that these groups shared some floristic features and some Irish pinewoods may be transitional between them.

Although it did not correspond directly with the Scottish plots surveyed, Group 1 bore some similarity to the NVC W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland type (Rodwell, 1991b) and the 'old sessile oak woods with *Ilex* and *Blechnum* in the British Isles' (91A0) category on Annex I of the EU Habitats Directive (EEC, 1992). In broader phytosociological terms, Group 1 fitted into the *Pino-Quercetum* (mixed pine-oak forest) association of the alliance *Quercion robori-petraeae*, order *Quercetalia robor-petraeae* and class *Querco-Fagetea* (Kelly & Connolly, 2000). This association forms a transition from pine to acidophilous oak forest, from western Europe to eastern Poland. It is favoured on somewhat better soils and by increased oceanicity towards the Baltic coast (Rodwell & Cooper, 1995). In terms of Norwegian pine forests, Group 1 was related to the moderately poor, dry to mesic *Vaccinium myrtillus*-dominated type (Table 5.4). Its closest correspondence is with the mixed pine-oak forests that are relatively common in south-west Norway. With reference to the general associates and preferential species of Group 1 (Table 5.3), *Quercus petraea*, *Q. robur* and *Ilex aquifolium* can be important constituents of the *Vaccinium myrtillus* type in this area (Fremstad, 1997). *Luzula sylvatica* also has a marked oceanic affinity in Norway and can occur as a dominant species in poorer types. Elsewhere,

however, the *Vaccinium myrtillus* type reverts to the more typical birch-pine-bilberry forest described by Aune (1977) and this does not correspond fully to Group 1. *Rhododendron ponticum*, the differential species for Group 1, does not occur in Norway and many of the characteristic species of the Nordic *Vaccinium myrtillus* type were absent from the Irish Group 1 plots e.g. *Luzula pilosa, Trientalis europaea, Linnaea borealis, Maianthemum bifolia, Orthilia secunda, Pyrola media* and *Deschampsia flexuosa*.

Table 5.4. Major *Pinus sylvestris* forest types in the Nordic area in relation to moisture and nutrient gradients.

| **Moisture Gradient**<br>**Nutrient Gradient** | **Dry** | **Dry-Mesic** | **Mesic** | **Moist** | **Wet** |
|---|---|---|---|---|---|
| **Rich** | Xeric basiphilous | Herb-rich basiphilous | Seasonal hygric basiphilous | Moist basiphilous | Rich fen basiphilous |
| | - | - | - | - | Rich swamp basiphilous |
| **Moderately poor** | - | *Vaccinium myrtillus* | Small fern | - | - |
| **Poor** | Sandy soil *Calluna vulgaris* | - | *Calluna vulgaris-Vaccinium uliginosum* | Moist *Calluna vulgaris-Vaccinium uliginosum* | Poor swamp |
| | *Vaccinium vitis-idaea* | - | - | *Molinia caerulea* | Poor minerotrophic mire |
| | Lichen-rich | - | - | - | Bog |
| | Rock outcrop | - | - | - | - |

In Group 2, two Irish plots were merged with all but one of the Scottish plots, indicating a direct correspondence between some of the reintroduced Irish pinewoods and their high quality, native Scottish counterparts. The group is characterised by low mean species richness and low rock/gravel coverage, which may be related to the peaty substrates on which these plots occur.

The distinction within Group 2 may provide a basis for sub-division. The sub-group containing plots S26, I6 and I2 formed a 'tail' to the main group at relatively low values on Axis 3. Floristic data from the individual plots showed that *P. sylvestris*, *Calluna vulgaris*, *Vaccinium myrtillus*, *Empetrum nigrum*, *Erica tetralix* and *Eriophorum vaginatum* occurred in all three. *E. vaginatum* did not occur in any other plots in the dataset and is strongly indicative of bog habitats, confirming that these plots represented *P. sylvestris*-dominated bog woodland. The two plots located at the end of this 'tail' were both recorded in Ireland and had previously been classified as *Calluna vulgaris-Eriophorum vaginatum*, a *P. sylvestris*-dominated bog woodland vegetation type (Roche *et al.*, 2009). The remaining plot, which lay between the two Irish plots and the main cluster, was recorded in Scotland. Under the classification scheme used for SAC selection in the UK (McLeod *et al.*, 2005), it had previously been described as bog woodland (A. Amphlett, pers. comm.). The other sub-group, containing plots S22 to S25 and S27, formed a tight cluster about halfway up Axis 3 on the NMS ordination. The tight clustering of these plots on both the cluster dendrogram and NMS ordination suggested a consistent floristic composition. Floristic data from the individual plots showed that *P. sylvestris*, *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea* occurred in all five and *Deschampsia flexuosa* occurred in four. These are all constant species of the NVC W18 *P. sylvestris-Hylocomium splendens* woodland type (Rodwell, 1991b), the typical vegetation type of Caledonian forest (McLeod *et al.*, 2005).

The relationship between these Irish and Scottish pinewoods is of interest in assessing the conservation value of the reintroduced Irish stands. The placement

of Caledonian forest and *P. sylvestris*-dominated bog woodland plots within the same overall group suggests that they share a broad floristic similarity but the sub-grouping suggests that they are not closely comparable. *P. sylvestris*-dominated bog woodlands in the UK are described as intermediate in character between W18 *P. sylvestris-H. splendens* woodland and more open mire types such as M18 *Erica tetralix-Sphagnum papillosum* mire or M19 *Calluna vulgaris-Eriophorum vaginatum* blanket mire (Rodwell, 1991b, a; McLeod *et al.*, 2005). This accounts for the placement of bog woodland and Caledonian forest plots within the same group. The relative position of the sub-groups on Axis 3 is also informative. Axis 3 exhibits extremely significant correlations with slope and altitude (Table 5.2). According to McLeod *et al.* (2005), within the Cairngorms SAC, where S25 and S26 were recorded, the drier slopes and knolls support Caledonian forest and the hollows between contain wet mires with abundant bog woodland. This is borne out by the position of the *P. sylvestris*-dominated bog woodland plots at the lower end of Axis 3, indicating that they occur on flat topography at lower altitudes, while the Caledonian forest plots occur on sloping ground at higher altitudes.

In broader phytosociological terms, the Caledonian forest plots of Group 2 fitted into the *Hylocomio-Pinetum* association of the *Dicrano-Pinion* alliance (acid, sandy-soil pinewoods). The Irish bog pinewood plots fitted into the *Vaccinio uliginosi-Pinetum sylvestris* (bog pinewood) association of the *Betulion pubescentis* (birch and coniferous bog woodland) alliance. Although it was floristically very similar to the Irish bog pinewoods, the absence of *Betula pubescens* from the Scottish bog pinewood plot meant that it had to be placed in the *Eriophoro vaginati-Pinetum sylvestris* association of the *Sphagnion magellanici* (mire pinewood) alliance. All of these alliances fit within the order *Vaccinio-Piceetalia* and class *Vaccinio-Piceetea* (Kelly & Connolly, 2000). The *Vaccinio uliginosi-Pinetum sylvestris* association occurs on the scattered raised mires of eastern, central and northern Europe. These bog pinewoods often contain *Betula pubescens*, *Calluna vulgaris, Vaccinium myrtillus*, *V. oxycoccus*, *Andromeda polifolia* and *Eriophorum vaginatum* (Rodwell & Cooper, 1995), all of

which occurred in the Irish *P. sylvestris* bog woodland plots. In Fennoscandian terms, the floristic composition of the Irish *P. sylvestris*-dominated bog woodlands is closest to that of poor, wet wooded bogs (Table 5.4) in oceanic western Norway and, to a lesser extent, parts of southern Norway and western Sweden with a sub-oceanic climate (Aune, 1977). The strictly oceanic species *Erica cinerea* occurs only along the coastal fringe of western Norway. Bog pine forests can also be found in more continental parts of Fennoscandia, but with north-eastern species such as *Ledum palustre* in place of oceanic species.

The placement of reintroduced Irish and native Scottish bog pinewood plots within the same sub-group indicates that they are directly comparable in terms of their floristic composition. It is acknowledged that the sample size for bog pinewoods, particularly in Scotland, is very small. This reflects the rarity of this vegetation type (Fossitt, 2000; McLeod *et al.*, 2005) but may restrict the applicability of these findings. However, in this case at least, the reintroduced Irish bog pinewood plots seem to be analagous to a native, semi-natural ecosystem of high biological quality. Roche *et al.* (2009) classified the Irish bog pinewood plots as the *Calluna vulgaris-Eriophorum vaginatum* type and deemed them to be of conservation value due to their rarity, semi-natural character and close correspondence with Fossitt's (2000) bog woodland habitat type, a priority habitat under Annex I of the EU Habitats Directive (EEC, 1992). The close correspondence of this type with native bog pinewoods in Scotland and continental Europe supports this conclusion. In terms of the qualifying features for SAC selection in the UK (McLeod *et al.*, 2005), Clonfinane Bog (I2) in particular exhibits good structure with a range of age classes from regeneration to deadwood. As the Irish stands are non-relict, naturalising within the last 200 years (O'Connell & Doyle, 1990; Heery, 1993), their ecological stability is not fully understood and requires further research. Both Clonfinane Bog and All Saints Bog (I6) have already been designated as SACs, primarily because of the presence of active raised bog (7110) and, in the case of All Saints Bog, *Betula*-dominated bog woodland. However, the Irish bog

pinewoods seem to function as a native ecosystem and are therefore of conservation value in their own right.

Group 3 was composed entirely of Irish plots which had previously been classified as *Corylus avellana-Brachypodium sylvaticum*, a calcicolous pinewood type (Roche *et al.*, 2009). This group represented a distinct vegetation type (Fig. 5.3) with high species richness (Table 5.3). Its high rock/gravel coverage reflected the substrate of the plots – limestone pavement in I3, I13 and I20 and outcropping granite in I8. An extremely significant positive correlation suggested that rock/gravel coverage may act as an indicator of species richness in the pinewood vegetation communities studied.

Group 3 did not correspond to any of the plots recorded in Scotland, where limestone pavement is relatively uncommon and limited in extent (McLeod *et al.*, 2005). In broader phytosociological terms, this group fitted into the *Erico-Pinetea* class, *Erico-Pinetalia* order, *Erico-Pinion* alliance of calcicolous pinewoods. This alliance includes numerous associations, such as the *Erico-Pinetum sylvestris* and *Molinio-Pinetum* of the Alps, the *Echinosparto-Pinetum*, *Polygalo-Pinetum* and *Sabineto-Pinetum* of northern Spain and the variable *Convallario-Pinetum* of Fennoscandia (Rodwell & Cooper, 1995; Kelly & Connolly, 2000), where *P. sylvestris* forms communities on shallow limestone soils and floristic trends relate to moisture and nutrient gradients (Bjørndalen, 1980; Bjørndalen, 1985). Group 3 seems to correspond to the Fennoscandian *Convallario-Pinetum* association. Due to their complex nature, with different floristic and ecological elements occurring in subtle mosaics, Bjørndalen (1985) found that the classification of Fennoscandian calcicolous pinewoods using the European phytosociological system was unsatisfactory and proposed an alternative, synchorological approach based on moisture and nutrient gradients, which has been incorporated into Table 5.4. In terms of floristic composition, structure and ecology, Group 3 corresponded to the Nordic basiphilous pine forest types (Table 5.4) (J.E. Bjørndalen, unpublished). As in Fennoscandia, species from a variety of floristic-

ecological groups and phytogeographical elements were represented. At Ballykine (I20), for example, fragments of rich-fen stands with *Molinia caerulea* and *Schoenus nigricans* and other moist types were found in a complex, small-scale mosaic. Similar types are also known from Gotland in the Baltic Sea. With reference to Table 5.3, species such as *Ilex aquifolium, Hypericum pulchrum* and *Hypochoeris radicata* are common to both Irish and western Norwegian calcicolous pinewoods where they have an oceanic distribution. Species such as *Geranium sanguineum, Carex flacca, Prunus spinosa* and *Hedera helix* are restricted to the south, but occur from western Norway to the Baltic area. Oddly, *Sesleria caerulea* is a strictly south-eastern species in Fennoscandia and, in basiphilous pine forests, occurs only in the Baltic Sea islands, the Stockholm archipelago and Estonia. *Teucrium scorodonia, Arum maculatum, Potentilla sterilis* and *Thymus polytrichus* have not been recorded in Nordic basiphilous pine forests.

Group 4 merged five Irish plots and one Scottish plot (S21). The cluster dendrogram (Fig. 5.2) and NMS ordination (Fig. 5.3) showed little distinction between these Scottish and Irish plots, implying a fairly high level of floristic similarity. The lack of differential species for Group 4 may be related to its slight overlap with Groups 1 and 2 on the NMS ordination (Fig. 5.3a, c). Four of the five Irish plots were previously classified as *Galium saxatile-Agrostis capillaris*, an upland pinewood vegetation type (Roche *et al.*, 2009). Due to its high values on Axis 3 of the NMS ordination (Figs. 5.3 a, b), this group is associated with sloping topography at relatively high altitudes (Table 5.2). The floristic data for individual plots showed that S21 (Cona Glen) is distinguished from the other Scottish plots by relatively high abundances of *Molinia caerulea*, *Festuca ovina*, *Blechnum spicant* and *Potentilla erecta* and by the presence of *Galium saxatile*. These species have all been reported as being unevenly represented in the different sub-communities of *P. sylvestris-Hylocomium splendens* woodland in Scotland (Rodwell, 1991b). *M. caerulea* increases in frequency towards the west and indeed, S21 was the westernmost of the Scottish plots. *F. ovina* becomes more

frequent where there is consistent grazing. Unlike the other sites surveyed, Cona Glen is privately owned and is managed for commercial purposes with grazing by red deer, sheep and Highland cattle. *Galium saxatile* and *Festuca ovina* often occur on more fertile soils, however soil fertility was not analysed here. Differing environmental conditions and management practices may have produced the differences in vegetation that separated S21 from the other Scottish plots. Indeed, in their review of the coverage of the NVC, Rodwell *et al.* (2000) acknowledged that pinewoods with abundant *M. caerulea* are occasional in the Highlands and may warrant a new sub-community of the W18 *P. sylvestris-H. splendens* woodland type. The placement of the Irish *Galium saxatile-Agrostis capillaris* plots within the same group as this *M. caerulea*-dominated pinewood plot indicates that these reintroduced Irish plots are floristically similar to a putative sub-community of the native Scottish pinewoods.

The lack of differential species for Group 4 hindered its classification within the broader phytosociological framework. The frequency of *Vaccinium myrtillus*, *Calluna vulgaris*, *Sorbus aucuparia*, *Deschampsia flexuosa* and *M. caerulea* suggested that Group 4 fitted into the *Vaccinio-Piceetea* class, *Vaccinio-Piceetalia* order, *Dicrano-Pinion* alliance of heathy acid pinewoods (Rodwell & Cooper, 1995) but its corresponding association was unclear. This group was also more difficult to relate to the Nordic types. Moist, poor *M. caerulea* dominated pine forests are known from Norway (Fremstad, 1997), as shown in Table 5.4, but do not correspond strongly with Group 4. Fennoscandian pine forests that have been modified by grazing may contain grazing indicators or grassland species, such as *Galium saxatile* in western Norway.

Although Groups 1 and 3 did not correspond directly with the Scottish pinewoods surveyed, this is not to say that examples of these vegetation types do not occur in Scotland. Suitable environmental conditions exist there, although these types do not appear in relevant vegetation descriptions such as the NVC (Rodwell, 1991b), where the W18 *P. sylvestris-H. splendens* woodland type includes more natural

pinewoods, modified stands and plantations. In this study, native pinewoods of high biological quality were selected from the list of Scottish SACs designated for Caledonian forest and/or bog woodland, which are priority habitats under Annex I of the EU Habitats Directive (EEC, 1992), thereby excluding other Scottish pinewood vegetation types.

The list of Nordic pine forest types presented in Table 5.4 was used for comparative purposes. It was beyond the scope of this paper to describe each of these types, but the relevant sources are given for the types that were found to correspond with the Irish and Scottish plots. Future research will include a more comprehensive comparison between Irish, Scottish and Nordic pine forests using multivariate analyses of relevé data.

## 5.6 Conclusions

This research has demonstrated that the species composition of certain reintroduced pinewood vegetation types in Ireland resembles that of high quality, native, semi-natural pinewoods in Scotland and in continental Europe. Classification identified four main vegetation types. Group 1, the Irish *Vaccinium myrtillus-Ilex aquifolium* vegetation type, did not correspond to the Scottish plots. However, qualitative comparison linked it to the NVC W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland type (Rodwell, 1991b), the 'old sessile oak woods with *Ilex* and *Blechnum* in the British Isles' category on Annex I of the EU Habitats Directive (EEC, 1992), the *Querco-Pinetum* association and the Nordic *Vaccinium myrtillus* pine forest type. Group 2 was the main interface between the Irish and Scottish plots. The Irish *Calluna vulgaris-Eriophorum vaginatum* bog woodland type was shown to be floristically very similar to a native Scottish bog pinewood and broadly similar to native Caledonian forest, both of which are recognised as habitats of international conservation importance (EEC, 1992). Qualitative comparisons linked Group 2 to the *Vaccinio uliginosi-Pinetum*,

*Eriophoro vaginati-Pinetum sylvestris* and *Hylocomio-Pinetum* associations of continental Europe and to the Nordic bog pine forest types. Group 3, the Irish *Corylus avellana-Brachypodium sylvaticum* vegetation type, exhibited by far the highest mean vascular plant diversity observed in this study. Although it did not correspond to the Scottish plots, qualitative comparison linked it to the Fennoscandian *Convallario-Pinetum* association and other Nordic basiphilous pine forest types. Group 4 showed linkages between the Irish *Galium saxatile-Agrostis capillaris* type and a putative *Molinia caerulea*-dominated sub-community of W18 *P. sylvestris-H. splendens* woodland, the vegetation type typical of native Caledonian forest. However, due to a lack of differential species, it was not found possible to relate this group directly to a continental European type.

This study supported the conclusions of Roche *et al.* (2009) that reintroduced pinewoods represent an important resource for Ireland's botanical and habitat diversity and that the *Calluna vulgaris-Eriophorum vaginatum* type is of significant conservation value. In conclusion, Ireland's reintroduced pinewoods behave, to a greater or lesser extent, like native ecosystems in the nearest regions where such forests occur. This finding provokes questions about the validity, in this case, of the native/alien paradigm, which has informed many conservation and forest management strategies. For practical conservation purposes, it seems that *P. sylvestris* should be managed as a native species in Irish woodland habitats despite its apparently reintroduced status.

# 6. General Discussion

The main aim of this study was to contribute to an improved understanding of the ecology, native status and biodiversity value of *P. sylvestris* in Ireland. This was achieved using a range of biogeographical, palaeoecological and ecological approaches at varying scales. Firstly, I reviewed, analysed and mapped new and existing palaeoecological data on the postglacial dynamics of *Pinus* in Ireland. Secondly, I examined the late Holocene vegetation history of a naturalised pinewood in the Burren. Thirdly, I described the vegetation ecology of pinewoods in Ireland and assessed their conservation value. Finally, I compared these pinewoods with their native counterparts in Scotland and continental Europe, placing them within the broader phytosociological context. In this final chapter, I will summarise the results of these investigations, compare my findings to previous research, explore the limitations and implications of this study and make suggestions for future research.

## 6.1 Summary and Synthesis

Clarification: This study indicates that a population of *P. sylvestris* persisted through the late Holocene at Rockforest in western Ireland and that *P. sylvestris* should therefore be regarded as a native species in Ireland. Based on its functional ecology, *P. sylvestris* should be managed as a native species within Irish woodland habitats for *practical conservation purposes*. However, it must be remembered that *P. sylvestris* underwent a massive decline in Ireland and, in the national sense, must have been at biologically insignificant levels throughout the historic period (Speight, 1985; Bradshaw & Browne, 1987). Irish *P. sylvestris* populations, with the possible exception of Rockforest, are still thought to originate from reintroduced stock and, unless proven otherwise, must be considered as *genetically*

non-native. Therefore, I will continue to use the term 'reintroduced' when referring to Irish *P. sylvestris* populations in the general sense.

### 6.1.1 Postglacial Dynamics and Palaeoecology of *P. sylvestris* in Ireland

Chapter 2 showed that *P. sylvestris* colonised Ireland by 10,500 cal BP, with its initial appearance seemingly occurring in the west of the country. Over the next three millennia, it migrated throughout Ireland. The establishment of forests with a significant component of *Pinus* was complete by about 8000 cal BP and the species reached its Holocene maximum at 7500 cal BP. This was followed by a progressive collapse in *Pinus* frequencies throughout most of Ireland. *Pinus* appeared to have been marginalised in lowland habitats from 7000-6500 cal BP, coincident with the *Alnus* expansion. The *Pinus* decline progressed from east to west and by 5500 cal BP, the species had been extirpated across large areas of Ireland. The decline continued as most of the remaining western populations appear to have been gradually extirpated. *Pinus* pollen frequencies reached their Holocene minimum at 2500 cal BP. At 2000 cal BP, the pollen record from Rockforest Lough opened. In contrast with other sites, it exhibited high *Pinus* pollen frequencies until 0 cal BP, indicating the persistence of a relict population. The reintroduction of *Pinus* from non-native sources was evident at 0 cal BP.

Chapter 3 examined the pollen record and other palaeoecological proxies from Rockforest Lough in more detail. They demonstrated a relatively stable vegetation history over the last two millennia, despite considerable human activity including partial woodland clearance, mixed farming and forestry. The dominant vegetation type was an open pinewood with abundant *Corylus*. Woodland cover appeared to be continuous throughout the study period although a gradual expansion of open ground, particularly grassland, was recorded. Remarkably, the *Pinus* decline was not recorded at this site, with *Pinus* pollen values continually exceeding 38% and macrofossil evidence demonstrating the local presence of *Pinus*. This indicates

that the *P. sylvestris* woodland at Rockforest is a relict population that has persisted to the present day. Chapter 2's isopoll maps provided support for this, showing elevated *Pinus* values at some other sites in the region during the late Holocene. Woodland continuity through the period prior to the Great famine of 1845 is unusual but may be attributable to management practices on Rockforest Estate.

Although Chapter 2's isopoll maps and correlation analyses generally supported the postglacial distribution patterns of *P. sylvestris* in Ireland described by other authors, the large dataset and multi-site perspective of the isopoll maps highlighted some new or previously poorly defined patterns. Previous studies are in agreement with the timing of the arrival of *Pinus* but suggest that *Pinus* first colonised south-west Ireland (Mitchell & Ryan, 1997; Mitchell, 2006), rather than the westerly location shown in the isopoll maps. The isopoll maps' representation of the migration of *Pinus* throughout Ireland and its subsequent decline is largely consistent with that described by previous studies, including the available isopoll maps (Bennett, 1984; Bradshaw & Browne, 1987; Bradshaw, 1993, 2001). Watts' (1984a) 1050 ± 160 cal BP date for the last recorded *Pinus* pollen and macrofossils at Gortlecka is consistent with the *Pinus* macrofossil from Rockforest Lough at 1110 ± 60 cal BP. This suggests that Watts' date was correct and that, at the time of its publication, the Gortlecka profile (and therefore the Burren, rather than midland raised bogs) supported Ireland's last known native population of *Pinus.*

The open pinewood with abundant *Corylus* described from Rockforest Lough is similar to those described from other sites in the Burren (Watts, 1984a; Feeser & O'Connell, 2009). However, in its clear suggestion of the persistence of a relict population of *Pinus* to the present day, this pollen record is in stark contrast with those from other Irish sites. Other possible causes for this unusual pollen signal (e.g. redeposition or inwash of eroded sediment) were considered but the available evidence suggests that the pollen record from Rockforest Lough is valid. In addition to the sites shown in the isopoll maps, some undated pollen records from

the Burren show elevated *Pinus* values during the period when the species was previously thought to be extinct (Crabtree, 1982; Watts, 1984a), lending support to the hypothesis of *Pinus* survival through the late Holocene. At a longitude of 8° 57'W, Rockforest appears to represent the western limit of the native range of *P. sylvestris*, as this was previously thought to occur in the north-west of the Iberian Peninsula at about 8°W (Jalas & Suominen, 1973; Willis *et al.*, 1998).

### 6.1.2 Vegetation Ecology of *P. sylvestris* in Ireland

Chapter 4 demonstrated that *P. sylvestris* has broad environmental tolerances in the Irish landscape. It occupies a wide variety of substrates in Ireland including mor humus, blanket peat, limestone pavement and coastal dunes, tolerating soil pH values from 3.3 to 6.2. It has been seen to range in altitude from just above sea level to about 360 m. *P. sylvestris* is distributed throughout Ireland and is well established, well integrated and naturalising in semi-natural habitats including woodland, dry heath, raised bog and limestone pavement (J. Roche, personal observations). As the autecology of *P. sylvestris* in Ireland has not been adequately addressed in the literature, these findings must be compared with studies conducted at a broader perspective. The wide ecological amplitude of *P. sylvestris* in Ireland is consistent with its behaviour in Britain (Carlisle & Brown, 1968) and in continental Europe. As Ellenberg (1982) put it,

> "*It surpasses all other tree species in the multiplicity of habitats it occupies … everywhere Scots pine can find a sunny spot or uncontested corner*".

*P. sylvestris*-dominated woodland in Ireland is diverse, with four distinct vegetation types which, except for the presence of a reintroduced species in the canopy, are semi-natural in character. Furthermore, Chapter 5 demonstrated that each of the Irish pinewood vegetation types corresponds, to a greater or lesser extent, to native pinewood types in Scotland or continental Europe. This suggests

that Irish pinewoods function as native ecosystems, despite the reintroduced status of the dominant tree species. Given Ireland's impoverished flora and low coverage of woodland, not to mention native woodland, these communities form a significant resource for the conservation of Ireland's native botanical and habitat diversity. For practical conservation purposes, it seems that *P. sylvestris* should be managed as a native species in Irish woodland habitats despite its reintroduced status.

Since these modern pinewoods form a significant resource for the conservation of Ireland's native botanical and habitat diversity, it is likely that they also support a wide variety of non-vascular plants and faunal species. For example, red squirrels (*Sciurus vulgaris*) were observed in the pinewood canopy at the Vale of Clara and Derrycrag (J. Roche, personal observation). Indeed, studies have shown that in coniferous woodland red squirrels have higher survival rates than grey squirrels (*Sciurus carolinensis*), which are non-native and invasive in Ireland (Kenward *et al.*, 1998; Ó Teangana *et al.*, 2000). Interestingly, the red squirrel is also thought to have undergone extirpation and reintroduction in Ireland (Ó Teangana *et al.*, 2000) and is the subject of an All-Ireland Species Action Plan (Anon., 2008). A study of the fungi associated with *P. sylvestris* woodlands in Ireland is also being conducted (O'Hanlon & Harrington, 2009).

Some important distinctions must be drawn between modern Irish pinewoods and their ancient counterparts. Although pinewoods are widespread throughout Ireland today, they are fragmented and limited in extent in comparison with their former range. The majority of modern Irish pinewoods originated as plantations and many are managed for commercial forestry purposes, so they are relatively modified in nature. There is also the issue of infestation with the non-native *Rhododendron ponticum*, which was found to be particularly pernicious in pinewoods in the south-west of the country. Finally, the biodiversity associated with Irish pinewoods has been impacted by the extirpation of faunal species such as the capercaillie (*Tetrao urogallus*) (van Wijngaarden-Bakker, 1985) and a suite

of *Pinus*-dependent saproxylic invertebrates (Speight, 1985; Whitehouse, 2006; Reilly, 2008).

## 6.2 Relevance of the Research

### 6.2.1 Methodological Considerations

In this study, various methods were employed at different spatial and temporal scales to investigate the ecology, native status and biodiversity value of *P. sylvestris* in Ireland. In evaluating the relevance of the research presented here, the methodological limitations must be considered and some particularly useful methodological approaches should be highlighted.

The assumptions and methodological limitations associated with isopoll maps have already been discussed in detail in Chapter 2, primarily in Section 2.3.4.

In analysing the database of *Pinus* pollen frequencies and site attributes in Chapter 2, it would have been illuminating to test for significant differences, between different time periods and between high and low altitude sites for example. However, the format of the data was incompatible with such analyses. The data were non-normally distributed due to the high numbers of zero values, the number of samples varied among time intervals resulting in missing values and some of the data fields were in categorical rather than numerical format. Consequently, the non-parametric Spearman rank correlation technique was considered to be the most appropriate option. Although correlations do not necessarily represent causal relationships, they can be used to provide statistical support for the observed trends, such as the marginalisation of *Pinus* in lowland areas coinciding with the expansion of *Alnus* from 7000-6500 cal BP.

Spatial interpolation using GIS was found to be an effective and objective method of isopoll mapping. The GIS allowed great flexibility in the presentation of the maps. For example, different layers of data could easily be added or removed. The GIS-derived maps were effective in generating hypotheses on spatial and temporal distribution changes which could be further investigated using standard statistical approaches.

The pollen record from Rockforest Lough opened at 2000 cal BP with elevated arboreal pollen values, which have been interpreted as a probable representation of the Late Iron Age Lull. To confirm this, however, it would be necessary to extend the record further to investigate whether arboreal pollen values were relatively low prior to this time period.

The high *Pinus* pollen frequencies observed through the late Holocene from Rockforest Lough are unique among Irish pollen diagrams. Due to financial and time constraints, it was not possible to carry out pollen analysis and dating on more than one core. However, the examination of replicate cores would have been useful in further testing the hypothesis of continued survival of *P. sylvestris* through the late Holocene at this site.

As a result of the site selection criteria used, the conclusions drawn from the vegetation surveys of modern pinewoods in Ireland (Chapters 4 and 5) apply only to mature, uninvaded stands where *P. sylvestris* is dominant or co-dominant with native tree species. Although it is acknowledged that most of Ireland's pinewoods are reintroduced and modified in nature, the site selection criteria ensured that the stands surveyed represented natural conditions as closely as possible. Stands with frequent non-native or invasive species, which may transform the structure and species composition of the habitats in which they occur, were avoided so that it was the ecology of *P. sylvestris* under investigation rather than the ecology of a non-native or invasive species. Mature stands were selected to ensure that the

vegetation communities surveyed were not merely a transitional stage in the forest cycle.

Due to financial and time constraints, it was only possible to survey 18 sites (20 plots) in Ireland and six sites (7 plots) in Scotland. Although the survey is thought to have encompassed a representative sample of the variation in Irish pinewoods, this is a relatively small sample number. The sample number of bog pinewoods (two in Ireland, one in Scotland) was particularly small, due in part to the rarity of that particular habitat. This may restrict the applicability of the relevant findings.

When recording vegetation data, vascular plants were recorded on the Domin scale. This presented some issues for multivariate analysis. The Domin scale is not strictly compatible with certain data analysis techniques, such as Indicator Species Analysis (Podani, 2006), so the traditional synoptic table approach was employed. The bryophyte data in presence/absence format could not be amalgamated with the vascular plant data on the Domin scale and so were omitted from the analysis. In hindsight, the use of a percentage scale for vegetation data recording of vascular plants and bryophytes would have circumvented these problems. However, bryophyte frequency data were included in the synoptic table to provide additional detail on the vegetation associated with each group and to facilitate comparison with phytosociological syntaxa.

The analysis of the $\alpha$-diversity of each stand was restricted to the data available from five 4 $m^2$ quadrats within a 400 $m^2$ area. The quadrats were not distributed throughout the full extent of the stand. However, each 400 $m^2$ plot was subjectively placed to be representative of the stand as a whole.

Assessments of the effects of forest plantations on biodiversity should ideally include a comparison with the land use they are replacing (Smith *et al.*, 2006; Stephens & Wagner, 2007). The biodiversity of the plantation throughout the forest cycle should also be considered (Smith *et al.*, 2005; French *et al.*, 2008).

However, such a study did not fit within the remit of exploring issues surrounding the native status of *P. sylvestris* in Ireland.

Due to time constraints, limited availability of suitable data and the language of many of the relevant publications, the comparison of the Irish and Scottish plots surveyed with continental European pinewoods vegetation types had to be conducted in a qualitative manner. The comparison is subjective as a result and should be considered as a brief overview rather than a comprehensive review.

### 6.2.2 Implications and Practical Applications of the Research

*Palaeoecology*

The isopoll maps, mean *Pinus* pollen frequencies and database of regional postglacial pollen sequences presented in Chapter 2 may provide a useful resource for future palaeoecological research in Ireland. The isopoll maps provide a convenient visual summary of regional patterns in *Pinus* dynamics throughout the Holocene while the mean pollen frequencies provide an overall estimation of *Pinus* abundance throughout the country. The database of pollen sequences could be utilised as a basis for meta-analyses of other taxa. Chapter 2 should serve as an update to Bradshaw & Browne's (1987) review of the changing patterns in the postglacial distribution of *P. sylvestris* in Ireland.

The *Pinus* pollen signal presented in Chapter 3 should be kept in mind in the interpretation of late Holocene *Pinus* pollen records from other Irish sites, particularly in the Burren. Where *Pinus* pollen signals were recorded between the Medieval period and the reintroduction of *P. sylvestris*, the presumed extinction of *Pinus* in Ireland led some authors to question the validity of their dating analyses (Watts, 1984a) or suggest that redeposition or long distance transport may have occurred (Crabtree, 1982) rather than consider the presence of *Pinus*. It may be

necessary to interpret such studies in light of the findings presented here, particularly if they were conducted in the Burren. Chapter 3 should supplement Watts' (1984a) account of the Holocene vegetation of the Burren. Palynological databases were invaluable in the compilation of the database of pollen records presented in Chapter 2. In order to facilitate future research, the relevant metadata, palynological and chronological records will be submitted to the Irish Pollen Database.

The modern pinewoods surveyed during the course of this study may represent modern analogues of their ancient counterparts. The vegetation description provided in Chapter 4 may therefore be useful to palaeoecologists in the interpretation of pollen sequences from woodland vegetation. The pinewoods on limestone pavement have been shown to be modern analogues of a vegetation type that has occupied the Burren and other karstic areas in Ireland since the early Holocene. The bog pinewoods may represent a modern analogue of those that are thought to have occupied Irish raised bogs until their presumed extirpation at 1550 ± 140 cal BP (McAulay & Watts, 1961). The mixed pine-oak woodlands of the *Vaccinium myrtillus-Ilex aquifolium* type may represent a modern analogue of those that are thought to have occurred at Derrycunnihy Wood, Killarney until about 2000 years ago (Mitchell, 1988).

Palaeoecological records provide a valuable long-term perspective on the dynamics of contemporary ecosystems and on the relevant spatial and temporal scales for ecological restoration, but have been largely ignored in conservation-related research. However, with the increasing availability of palaeoecological data of high spatial and/or temporal resolution, there is potential for synergy between palaeoecology and conservation biology (Willis & Birks, 2006). This study illustrates that synergy in three main ways, which are discussed in more detail elsewhere in this chapter. Firstly, the meta-analysis of palaeoecological data (Chapter 2) provides information on the ecology, past distribution and abundance of *P.* sylvestris, which could be informative in the restoration of Ireland's native

woodlands e.g. in site and/or species selection. Secondly, palaeoecological techniques have been used to determine the native status of *P. sylvestris* in Ireland (Chapter 3), thereby resolving an issue related to biodiversity conservation. Finally, the study of the vegetation ecology of contemporary pinewoods in Ireland (Chapter 4), which are modern analogues of ancient pinewoods, can inform palaeoecological reconstructions of woodland vegetation.

*Vegetation Ecology*

This study indicates that *P. sylvestris* is native to Ireland and that, although most Irish pinewoods are derived from non-native stock, they are semi-natural in character and function as native ecosystems. If further studies corroborate the species' native status, future maps of its native range should extend its western limit to western Ireland. Future surveys and classifications of native woodland vegetation should include *P. sylvestris* woodlands. The vegetation descriptions and comparisons presented in Chapters 4 and 5 should therefore serve to supplement those of White & Doyle (1982) and Perrin *et al.* (2006; 2008a). In order to facilitate future research, the relevant metadata and vegetation data will be submitted to the National Vegetation Database of the National Biodiversity Data Centre.

*Forest Management*

The findings presented throughout this thesis support the decision to include *P. sylvestris* in Ireland's Native Woodland Scheme (NWS) and some of the outputs have practical applications therein. As discussed above, any vegetation classifications pertaining to the NWS should include *P. sylvestris* woodland and could incorporate the vegetation classification presented in Chapter 4. The isopoll maps showing the former range of *P. sylvestris* in Ireland and the quantitative data on the species composition and environmental attributes (altitude, slope, soil pH and soil organic content) of contemporary *P. sylvestris* woodland vegetation types

presented in Chapters 2 and 4 may be useful to the ecologists and foresters involved in drawing up NWS plans. These data could inform site selection for new plantings of *P. sylvestris* and species selection at given sites. As the NWS promotes the planting of native tree species of local genetic provenance, the pines at Rockforest could be used as a seed source for this scheme (Forest Service, 2001). However, any seed collection would have to be compatible with the long-term conservation of the pinewood at Rockforest.

*Conservation*

The majority of the Irish sites surveyed (72%) are designated as Special Areas of Conservation (SACs) and therefore receive protection from damaging land uses under the EU Habitats Directive (EEC, 1992). This research has demonstrated that the four Irish pinewood vegetation types described represent an important resource for Ireland's native botanical and habitat diversity. The *Calluna vulgaris-Eriophorum vaginatum* bog pinewood type and the sub-group of the *Corylus avellana-Brachypodium sylvaticum* type found on limestone pavement are of particular conservation interest. This is not thought to be simply a result of *P. sylvestris* colonising a habitat that is of conservation value in its own right, as the vegetation of these pinewoods is distinct to that of the surrounding open raised bog or limestone pavement.

Ireland hosts a significant proportion of the total global resource of raised bog. Even so, woodlands on intact raised bogs, whether *P. sylvestris* or *Betula*-dominated, are rare in Ireland (Fossitt, 2000). The international conservation importance of bog woodland is reflected in its inclusion as a priority habitat on Annex I of the EU Habitats Directive (EEC, 1992). Despite their relatively recent origin (O'Connell & Doyle, 1990; Heery, 1993) and reintroduced status, the naturalised Irish bog pinewoods on Clonfinane Bog and All Saints Bog have been shown to function as native ecosystems, as their vegetation composition corresponds directly to that of native bog pinewoods of high biological quality in

Scotland and broadly to the *Betulion pubescentis* alliance of continental Europe. Both of these sites are designated as Special Areas of Conservation, primarily because of the presence of active raised bog and, in the case of All Saints Bog, *Betula*-dominated bog woodland. However, this research has shown that Irish bog pinewoods are of conservation value in their own right.

Limestone pavement is an internationally rare habitat and its conservation importance is reflected in its inclusion as a priority habitat on Annex I of the EU Habitats Directive (EEC, 1992). Although Kelly & Kirby (1982) described the phytosociology of Irish native woodlands over limestone, their account did not include *P. sylvestris*. Three pinewoods on limestone pavement were surveyed at Rockforest, Rockvale and Ballykine (Plot 20) and they exhibited the highest levels of species richness and $\alpha$-diversity recorded in this survey. For example, 72 vascular plant species were recorded within a 400 $m^2$ plot at Ballykine, County Mayo. These pinewoods correspond closely with native types in Fennoscandia, indicating that they function as native ecosystems. All of these sites have been designated as Special Areas of Conservation.

The pinewood at Rockforest should be the subject of intensive conservation efforts, as this research indicates that it is Ireland's only known stand of extant, native *P. sylvestris* and therefore represents an important part of Ireland's genetic heritage. As well as being part of the East Burren Complex SAC, the site lies within the Burren National Park and so is owned by the state and managed for conservation purposes. This should serve to prevent damaging land uses, such as the selective felling of taller straighter specimens of *P. sylvestris* that occurred when the site was privately owned (J. Cunningham, pers. comm.). As discussed above, this pinewood may provide a seed source for planting native stock of *P. sylvestris*. Although any seed collection would have to be compatible with the long-term conservation of the site, the translocation of some individuals may be beneficial in conserving the apparently extant *P. sylvestris* population. As a single population is more vulnerable to extinction, it would appear prudent to establish a

second population on a similar site, identified by studying the ecological requirements of the original population (Maunder, 1992).

*Restoration Ecology*

The example of the reintroduction of *P. sylvestris* in Ireland is broadly relevant in the restoration of forest ecosystems elsewhere. There have been numerous other cases where dominant canopy tree species have undergone major declines through part of their range. In the early twentieth century, for example, American chestnut (*Castanea dentata*), a dominant species in eastern North American forests, was essentially extirpated as a canopy species by an introduced pathogen (Jacobs, 2007). A breeding programme has succeeded in developing a blight-resistant hybrid of *C. dentata* and Chinese chestnut (*C. mollisima*) (Diskin *et al.*, 2006). With the prospect of hybridized *C. dentata* reintroduction imminent, the associated potential long-term ecological implications must be determined (Jacobs, 2007). The successful reintroduction of *P. sylvestris* (which, like *C. dentata*, is a generalist adapted to a relatively wide range of environmental conditions) in Ireland may be informative in this context.

## 6.3 Future Research

The findings of this research present a wide variety of new research opportunities:

- The presumed extirpation of *P. sylvestris* in Ireland previously precluded the possibility of sampling native populations for the purposes of molecular analysis (Huntley & Birks, 1983; Sinclair *et al.*, 1998). However, recent advances, including the findings presented here, offer new opportunities in this field. The apparently native population of *P. sylvestris* identified in the present study may form the basis of a number of interesting studies in molecular ecology. The genetic structure of the population could be

determined, thereby informing conservation objectives for the site, such as translocation. Phylogeographic techniques could also be used to infer the provenance of the population, in a manner similar to the study conducted by Kelleher *et al.* (2004) on oaks in Ireland. This would be informative, firstly, in further testing the hypothesis of the continued survival of a native population of *P. sylvestris* through the late Holocene and, secondly, in determining which glacial refugium the population originates from and the postglacial migration route of *P. sylvestris* into Ireland. Sinclair *et al.* (1998) hypothesised that populations of *P. sylvestris* in western Scotland exhibiting distinct nuclear genetic markers originated from a different glacial refugium to those elsewhere in Scotland and migrated there via Ireland. The availability of genetic material from an apparently native *P. sylvestris* in Ireland means that this hypothesis can now be empirically tested. A major recent advance is the discovery that DNA from 10,000 year old fossil *Pinus* pollen preserved in lake sediments can be recovered and analysed (Parducci *et al.*, 2005). It would be fascinating to conduct a genetic comparison of ancient (using *Pinus* pollen samples from Rockforest Lough and other Irish sites) and modern (the pinewood at Rockforest and populations from western Scotland) populations to examine their inter-relationships.

- During the period when *P. sylvestris* was considered to be extinct in Ireland, the *Pinus* pollen signal at Rockforest Lough is unusually strongly expressed, weakly expressed at the Carron Depression and Rinn na Mona and absent or intermittent at other sites in the Burren. To further test the hypothesis of the continued survival of a native population of *P. sylvestris* at Rockforest through the late Holocene, it would be informative to model pollen dispersal in the area surrounding the pinewood at Rockforest using HUMPOL (Bunting & Middleton, 2005) or POLLSCAPE software (Gaillard *et al.*, 2008). It would then be possible to check if the pollen dispersal pattern recorded at Rockforest Lough fits with the model

predictions for a sampling site at equal distance from a pinewood in a similar landscape.

- AMS dating has shown that the core retrieved from Rockforest Lough extends to at least 9970 ± 140 cal BP and may cover the full Holocene. For the purposes of this study, only the last two millennia of vegetation history were reconstructed. Given the early appearance of *Pinus* in the Burren and the unusual history of *P. sylvestris* at this site, it would be interesting to extend this vegetation reconstruction so that it spans the full Holocene.

- A similar pollen study should be conducted at one of the other lakes in the vicinity of Rockforest, in order to further test the hypothesis of the continued survival of a native population of *P. sylvestris* in the Burren through the late Holocene. Palaeoecological analyses of proxies such as preserved insect fragments, non-pollen palynomorphs (e.g. *Pinus*-dependent fungi) and, of course, stomata may also be informative.

- As previously discussed, the modern bog pinewoods and mixed pine-oak woods surveyed may represent modern analogues of their ancient counterparts. The dynamics of modern and ancient pinewoods could be compared using fine spatial-resolution pollen analysis, modern pollen analysis and vegetation surveys.

- This study has highlighted the conservation value of pinewoods on raised bog and limestone pavement in Ireland. Since the completion of the botanical field surveys, other suitable sites have come to light. Surveys of additional sites would provide further information on the distribution and conservation status of these vegetation types and increase the sample size of the available data, which was a particular issue for bog pinewoods.

- The biodiversity value of the apparently native pinewood at Rockforest should be established through additional ecological surveys. For example, a suite of *Pinus*-dependent saproxylic invertebrates of the orders Coleoptera and Diptera are thought to be extinct in Ireland (Speight, 1985; Whitehouse, 2006; Reilly, 2008). It may therefore be interesting to investigate the invertebrate fauna of this site.

- Data were collected on the structure, regeneration and lichen flora of Irish pinewoods but were not fully incorporated in the analyses presented here. These datasets would be useful in further ecological studies and in predicting successional changes in Irish pinewoods and should be utilised.

- The vegetation data from Irish pinewoods were qualitatively compared with vegetation descriptions of Irish native woodland types and with phytosociological syntaxa from continental Europe. However, multivariate analyses of relevé data from these vegetation types would permit a more comprehensive and objective assessment of Irish pinewoods within their Irish and European context. The National Survey of Native Woodlands has recently been completed. One of its outputs is a database of 1667 relevés from native woodlands in every county in Ireland (Perrin *et al.*, 2008b), which could be used in this research.

- To further examine the biodiversity value of *P. sylvestris* plantations in Ireland, a study could be conducted comparing the biodiversity of the plantations with the land use they are replacing, as recommended by Stephens & Wagner (2007). The biodiversity of *P. sylvestris* plantations throughout the forest cycle could also be investigated.

## 6.4 Concluding Remarks

*Pinus sylvestris* is well established and naturalising in Ireland. Although they are fragmented and limited in extent compared to the species' former range, *P. sylvestris* plantations and, to a lesser extent, naturalised woodlands are a common feature of the Irish landscape. This study has shown that an apparently native population persists at Rockforest in the Burren, western Ireland. With the possible exception of Rockforest, populations of *P. sylvestris* in Ireland are thought to originate from non-native, reintroduced stock. Despite their reintroduced status, they have been shown to function as native ecosystems and form an important resource for the conservation of Ireland's native botanical and habitat diversity. For practical conservation purposes, *P. sylvestris* should therefore be managed as a native species in woodland habitats in Ireland. To conclude, *P. sylvestris* offers forestry potential, broad ecological tolerances, native status and the potential to support native biodiversity in the Irish context. *P. sylvestris* therefore has the potential to make a significant positive contribution to biodiversity conservation and sustainable forest management in Ireland and should be utilised as such.

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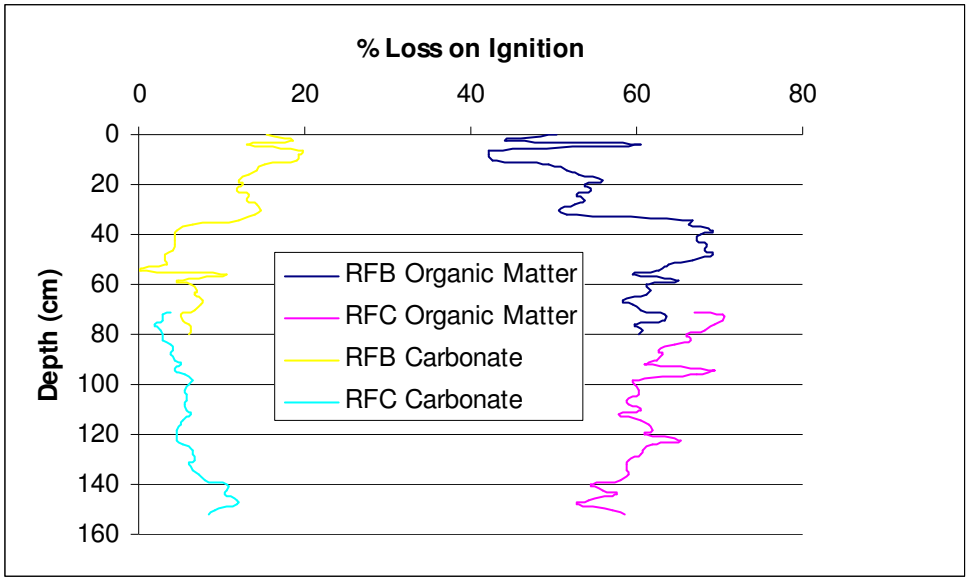
# Appendices

Appendix 2.1. Microsoft PowerPoint slideshow of isopoll maps of *Pinus* in Ireland from 11,500-0 cal BP. Refer to DVD attached to inside back cover.




Appendix 3.1. Percentage loss on ignition profiles for organic matter and carbonate for Rockforest Lough, showing separate curves for the RFB and RFC cores. These curves were used in core matching. Note the closely matched patterns in the overlapping sections of the curves.

Appendix 4.1. Refer to Fig. 2 in the following manuscript. Published as: Roche, J.R., Mitchell, F.J.G. & Waldren, S. (2008) Ecology of Scots pine (*Pinus sylvestris* L.) in Ireland – preliminary results. *Proceedings of the 17th Irish Environmental Researchers' Colloquium, Environ07, Institute of Technology Carlow, 26-28 January 2007* (ed. by R. Moles), pp. 6-9. Environmental Sciences Association of Ireland, University of Limerick, Limerick.