The development of Ireland's tree cover over the millennia

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Abstract
Ireland is not only the least wooded country in Europe, it also has the lowest forest biodiversity. Despite this, forest research repeatedly demonstrates that Ireland is one of the most favourable locations for growing trees in Europe. Augustine Henry was acutely aware of these issues which provided a stimulus for his promotion of Irish forestry. Yet Irish forests have not always suffered such paucity. The further back we go in time, the greater the forest cover and diversity we discover. This paper traces the decline of Irish forests over many millennia and addresses the principal causes of this decline.

Global climate change, human exploitation and geographical isolation are all contributory factors. The repeated glacial-interglacial cycle of climate change over the last two million years has decimated tree diversity in north-west Europe. The degree of Ireland's isolation from Europe has varied as sea levels have changed in tandem with global ice volume. This has influenced tree migration rates and direction but the Irish Sea should be considered as a filter rather than a barrier to tree migration. Recent analysis of a large fossil pollen database is used to illustrate the migration of forest trees into Ireland following the most recent deglaciation. These migration models are compared to newly emerging genetic data on European and Irish oak diversity. Human exploitation of Irish forests over several millennia has radically reduced the amount of forest cover and has significantly impacted on what remains. Reconstructions of forest composition are used to place contemporary Irish forests in context. This context is relevant both to the maintenance of existing forests and the establishment of new ones.

Keywords: forest cover, climate history, biodiversity, hazel, pine, elm, oak, human impact

Introduction
Ireland has the lowest forest cover in Europe after Iceland and this is coupled with one of the lowest biodiversities in the temperate zone. This contrasts with historical and palaeoecological data indicating that forest cover in Ireland in the past was far more extensive while fossil data suggest that biodiversity was higher in recent geological times and on a par with the rest of Europe.

In the early years of the twentieth century, Augustine Henry recognised the strategic importance of increasing the national forest while also realising that Ireland had an ideal climate for growing trees (Pim 1966). Subsequent forest research has repeatedly shown that Ireland is one of the most favourable locations for growing trees in Europe. The mismatch of this potential and the reality in terms of forest extent and diversity in Ireland will be explored in this paper by tracing the history of Irish forests back two million years.

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Today's forests

Forest cover in Ireland today is around 9% of the land surface. This has risen from an estimated 1% when Augustine Henry was promoting Irish forestry some eighty years ago. The increase has primarily been due to planting of exotic conifers on marginal land in upland areas. This planting policy reflects the land that was made available for forestry and the recognition, by Henry and others, of the suitability of west coast North American conifers to Irish conditions. The nearest examples of the original forest are represented by ancient woodland, i.e. sites that have maintained woodland cover since at least AD 1600 (Peterken 1981). It is recognised within this definition that these sites would have been subjected to silvicultural management in the past which may have included clearfelling. Ancient woodland cover in Ireland in 1830 was 0.2% and is considerably less than that today (Rackham 1995). Although this is a small resource, its importance lies in the direct link with the prehistoric primeval forest. It is evident from historical and palaeoecological research that no primeval or virgin forest exists in Ireland and it is debatable whether any exists in Europe (Mitchell 1995, Peterken 1996).

Webb (1983) has reviewed the vascular plant biodiversity of Ireland in a European context. He found that Ireland has 815 native vascular species compared to 1172 in Britain and 3500 in France. Data for fauna follow a similar trend. Trees represent a subset of the vascular plant data which also follow a similar trend. Ireland boasts 13 native tree genera, Britain has 18, western Europe has 22 and eastern USA has 51 genera (Ellenberg 1988, Petrides 1998). The reasons behind this low biodiversity in Ireland must be explored from several directions.

The availability of suitable habitats is perhaps of most immediate relevance. In the above comparison, Ireland is a small landmass compared to its neighbours; it also has the most uniform climate. This therefore restricts the availability of diverse habitats and Webb (1983) has argued that about 50% of the vascular plant species absent from Ireland that occur in Britain are excluded on ecological grounds; either they require a more continental climate or are high-altitude alpines. This still leaves a considerable number of species that have the potential to grow in Ireland but are not part of the native flora. Consideration of Ireland's geographic isolation and climatic history will be used to explore its biodiversity.

Climate history

Twenty thousand years ago Ireland was in the grip of an ice age, the Last Glacial Maximum (Mitchell and Ryan 1997). Ireland was almost totally covered by ice; if any areas did remain ice free, they certainly would not have supported trees. In fact there are no available data to support the presence of plant or animal life in Ireland during the Last Glacial Maximum. This time is a convenient starting point when considering the development of Irish forests because we know that all the trees had to migrate into Ireland after this time. However, the Last Glacial Maximum was not an isolated event. The analysis of deep ocean sediment cores which have accumulated slowly over two million years reveal that global climate has been punctuated by successive alternating cold glacial stages, similar to the Last Glacial Maximum, separated by warmer interglacial stages, with climates similar to today (Lowe and Walker 1997). Older geological records suggest that before two million years ago, the Tertiary period was climatically more stable, with Ireland enjoying a warm temperate to sub-tropical climate (Tallis 1991).

So the migration of forest trees into Ireland is not a unique event because Quaternary (the last two million years) climate has generated these conditions on numerous occasions in the past. It is therefore instructive to examine the floras of previous interglacials. Tallis (1991, Figure 10.1) has collated data which illustrate the number of tree genera present in north-west Europe at the end of the Tertiary (c. 2 million years ago) and their subsequent reduction in successive interglacials down to the present. This is an excellent illustration of natural selection where the 17 tree genera present in the current interglacial (the Holocene) are derived from an initial population of 47 genera at the start of the Quaternary. Tree genera that were able to migrate in response to rapid climate changes had an obvious advantage; the other genera became extinct in north-west Europe.

Coxon and Waldren (1997) review the Irish interglacial records in the context of the north-west European data but their review is restricted due to the very poor record of Irish Quaternary interglacials. Detailed palynological data are only available from a single site (Pollnahallia, Co Galway) from late Tertiary/early Quaternary times (Coxon and Flegg 1987) which can be contrasted with the unrivalled data from the Gortian interglacial (mid Quaternary) (Coxon 1996). There are substantially less tree genera in Ireland today compared to the Gortian; in this respect, the limited Irish data concur with Tallis's more comprehensive compilation for north-west Europe. However, it is important to note that about one third of the Holocene (present interglacial) tree genera that reached northwest Europe did not gain access to Ireland. These are the genera that have been selected over two million years of migration in response to the fluctuating Quaternary climate. They were all present in Ireland during the Gortian interglacial yet they failed to gain access during the Holocene. This suggests that Ireland was a particularly difficult place to get to after the Last Glacial Maximum. Similar parallels have been drawn with fossil fauna data in Britain (Sutcliffe 1995).

Migration

It is thus evident that, compared to the present day, Irish forests had considerably higher biodiversity in previous interglacials and, almost certainly, even higher biodiversity during the Tertiary. Although climate change is clearly associated with these discrepancies, it is migratory ability that is the key factor in determining the biodiversity of forest trees in north-west Europe. Climate change is merely the trigger that drives trees to migrate.

Migration routes into Ireland have traditionally been postulated to be from the continent, across Britain and then into Ireland (Mitchell and Ryan 1997). There has also been much debate about the role of land bridges and the filling of the Irish Sea (Devoy 1985, 1995). Experience from more remote islands, e.g. in the mid Pacific Ocean, informs us that trees are capable of long distance migration over water but that the mechanisms are rarely observed. In the Irish context, it probably more reasonable to consider our surrounding seas as filters rather than barriers to tree migration; in other words, some trees get across the sea while others do not. It is perhaps more profitable to consider the data that provide evidence for migration rather than speculating on the mechanisms of migration.

Radiocarbon dating of pollen diagrams provides a means by which the arrival of trees in the landscape can be determined. Recent research has significantly increased the number, and spread, of sites where this is possible in Ireland. It is now feasible to map tree arrival times on a national scale (Mitchell in press). Contouring of these maps provides images of arrival time as well as direction and rate of migration (Figure 1). The earliest tree to migrate into Postglacial Ireland was birch. Its almost instantaneous arrival

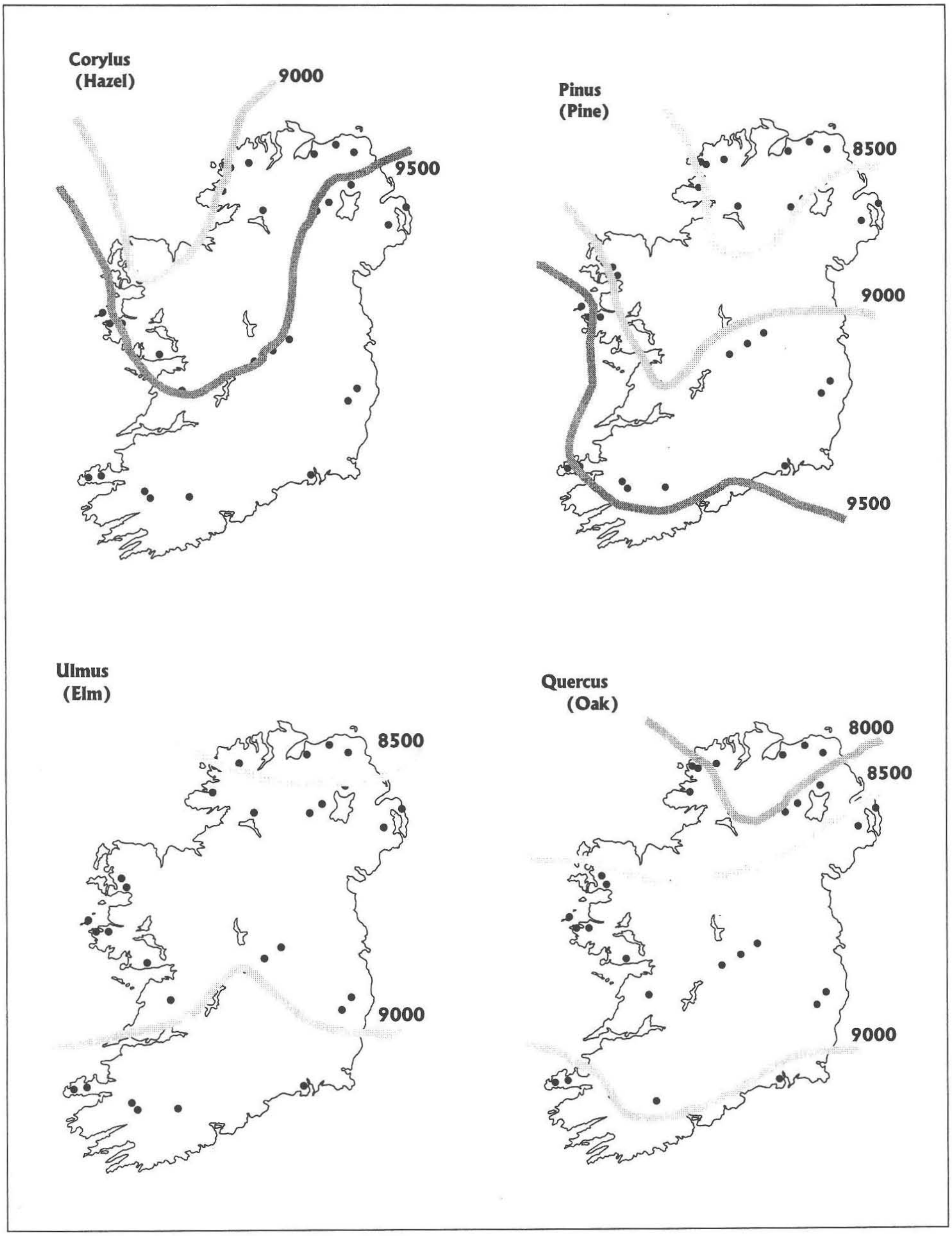

Figure 1. *Isochrone maps of Ireland for* Corylus, Pinus, Ulmus *and* Quercus *with isolines drawn at 500 radiocarbon year intervals from (Mitchell, in press).*

across the country defies mapping and indicates that this tree did not have far to travel. The next arrival was hazel which had a clear pattern of spread (Figure 1). It migrated in a north-westerly direction with a migration route into Ireland that could have been both across the Irish and Celtic Sea basins. Hazel was followed by pine, oak and elm which all migrated in a northerly direction (Figure 1). They appear to have entered Ireland across the south coast having traversed the Celtic Sea basin. The data provide no evidence that these trees crossed the Irish Sea. Furthermore, radiocarbon dates for arrival times of these trees in Britain are similar to those for Ireland (Birks 1989). If these trees had to migrate across Britain and the Irish Sea basin prior to their arrival in Ireland some time lag would be expected in the Irish dates.

It is also instructive to investigate trees that did not migrate into Ireland but that grow well here today. Beech and lime are both native to Britain but the pollen data indicate that they were late colonists. Lime crossed the English Channel after 8,000 BP and it arrived on the Welsh coast by 6,500 BP but has failed to cross the Irish Sea (Birks 1989). Beech was a much later migrant, not arriving in south east England until just before 3,000 BP. It arrived on the Welsh coast 1,000 years ago but, like lime, has failed to cross the Irish Sea (Birks 1989).

The pollen data enable a hypothesis to be developed which proposes that the earliest colonists (birch and hazel) gained access to Ireland from the east via the Irish Sea basin and from the south via the Celtic Sea basin but that the later colonists migrated in from the south only. Insufficient data are available to date the filling of the Irish Sea and Celtic Sea basins or to date the existence of land bridges across these seas (Devoy 1995). Wingfield (1995) has developed the hypothesis of a moving land bridge across the southern Irish Sea associated with crustal deformation caused by ice loading. This land bridge may have formed the conduit into southern Ireland for the later migratory trees (Mitchell in press).

Further evidence of migration routes comes from genetic data. A Europe-wide investigation of oak has identified a series of haplotypes derived from three glacial refugia: the Iberian peninsula, Italy and the Balkans (Dumolin-Lapègue *et al.* 1997). Although haplotypes from all three refugia spread across Europe during the Postglacial, so far only the Iberian haplotypes have been found in Ireland. This finding further strengthens the idea that trees were migrating up the Atlantic coast of Europe and into Ireland from the south rather than island hopping across Britain. Ongoing research into the genetics of Irish oak will provide improved resolution to the above work and explore differences between British and Irish populations.

Human impact

Humans have been in Ireland since at least 9,000 BP (Woodman 1978). Pollen and historical data demonstrate that they have had a profound impact on the landscape since the establishment of agriculture around 5,000 BP (Mitchell and Ryan 1997). The overall role that human populations have played in removing, transforming and replacing the native forests of Ireland have been discussed in detail elsewhere, not least in previous Augustine Henry Memorial lectures, and so will not be repeated here (Baillie 1999, Hall 1997, Kelly 1999, McCracken 1971, Mitchell and Ryan 1997, Mitchell 1995, O'Sullivan 1994). From these accounts it is clear that an island that was almost completely covered in forest in the early Postglacial was reduced to having a forest cover of less than 1% one hundred years ago as a result of human exploitation coupled with an oceanic climate. Over the last 100 years, major endeavours in afforestation have significantly increased our forest cover but

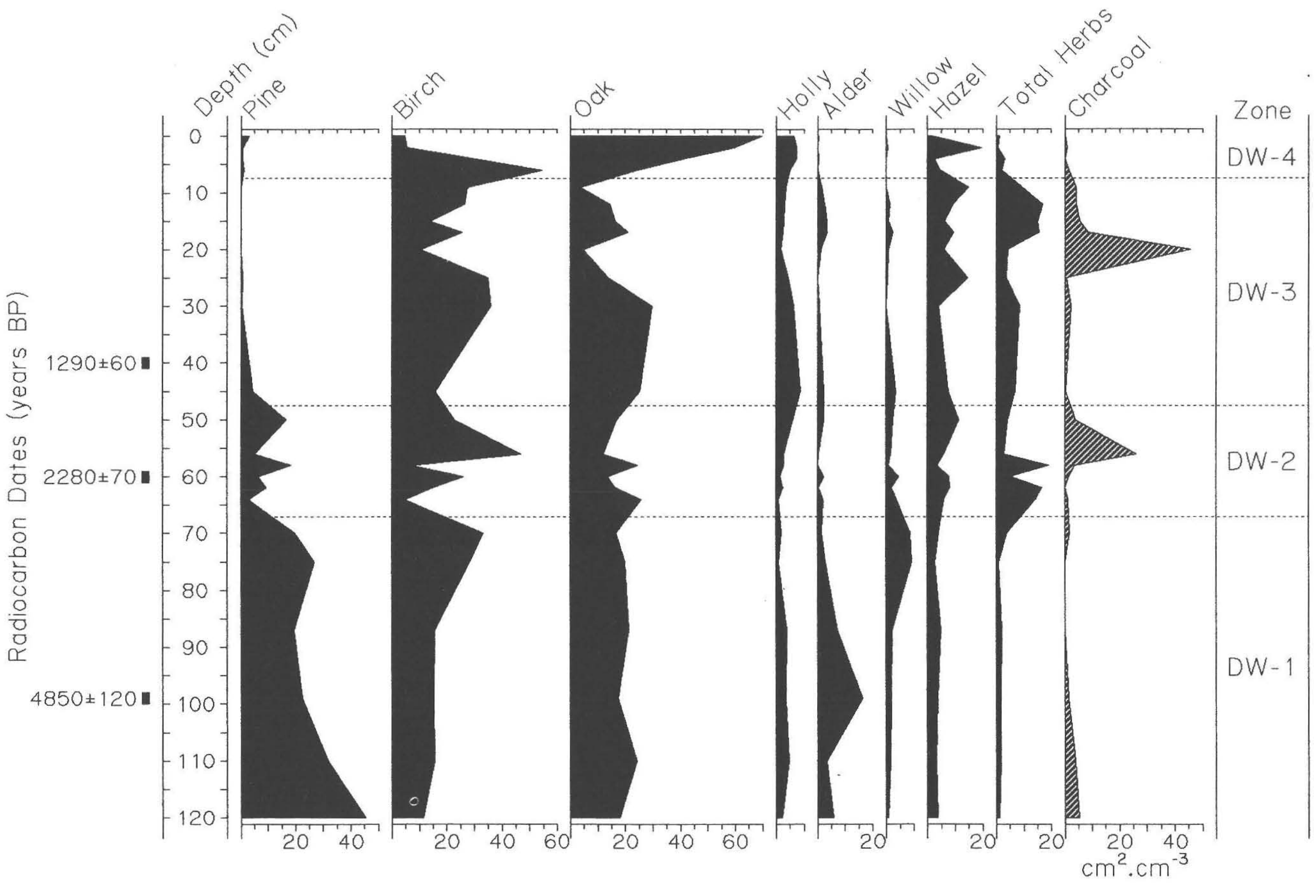

Figure 2. *Summary percentage pollen diagram from Derrycunihy Wood, Killarney redrawn from Mitchell (1988).*

less than 0.1% of land is covered by native ancient woodland – an irreplaceable link with the primeval forests that once covered the country. The importance of this resource cannot be over-emphasised and so to give it some context, it is useful to explore how human activities have impacted on it.

Traditional pollen analyses from bog and lake sediments provide reconstructions of vegetation on the landscape scale; they therefore lack the spatial resolution required to explore changes on the forest stand scale. Finer spatial resolution can be achieved by investigating small sites such as sediment-filled hollows under canopy woodland. Pollen analysis of such sites has been demonstrated to reconstruct vegetation at the forest stand scale (Mitchell 1998).

Derrycunihy Wood in the Killarney National Park is arguably the finest native oak wood in Ireland. Analysis of pollen from small ground hollows provides an insight into its history which catalogues past human impacts and provides a context for the wood today (Figure 2). Radiocarbon dating suggests that the record extends to before 5,000 BP and hence covers the period of principal human impact in Ireland. The oldest records indicate that the wood was dominated by a mixture of pine, oak and birch (Figure 2). Evidence from other small hollow sites on Old Red Sandstone in Killarney demonstrate that the proportion of pine to oak in the primeval forest was altitude dependent with almost pure pine at the highest altitude and negligible amounts at the lowest altitudes (Mitchell 1988, O'Sullivan 1990); Derrycunihy is at an intermediate position between these two extremes.

By 2,000 BP there was significant disruption to Derrycunihy Wood. This is highlighted by both the high charcoal values implying human-induced fire and the increase in abundance of herb pollen which indicates that the woodland canopy was sufficiently open to permit increased flowering of woodland herbs. These features in the pollen diagram are coupled with dramatic changes in the principal trees. Pine was eventually eradicated from the wood. This human-induced decline in pine has also been recorded in Uragh Wood on the Beara Peninsula at the same time (Little *et al.* 1996). The pine decline was also associated with significant fluctuations in oak and birch (Figure 2). The post-disturbance woodland that developed without pine was dominated by oak but was more open than its predecessor as indicated by the higher representation of birch, the understorey shrubs holly and hazel, and herbs.

Increases in charcoal and disturbances to the woodland canopy towards the top of the diagram relate to human activity in the eighteenth and early nineteenth centuries. This evidence for disturbance coincides with documentary records of charcoal production for iron smelting, timber extraction and grazing in Derrycunihy Wood (Young 1780). Assessment of the complete pollen records from Derrycunihy Wood and the other sites in Killarney indicate that, following disturbance, the botanical and structural diversity of the woods were reduced. The start of the nineteenth century saw the establishment of more comprehensive woodland management on the Killarney estates (Watts 1984). The pollen data record the recovery of the wood but with a disproportionate amount of oak. Oak was the most valuable tree of the time and so the silviculture of the time favoured it. At no time over the last 5,000 years has oak had such a dominance in Derrycunihy Wood. The dominance of oak in the Killarney woods today is thus a legacy of nineteenth century silvicultural practice rather than a reflection of the natural woodland composition. The reintroduction of pine to the region by eighteenth century foresters is also recorded in the upper levels of the diagram.

So while human exploitation has been responsible for the dramatic decline in Irish woodland cover over the millennia, it has also had a significant impact on the structure and composition of the small remaining patches of native woodland. Understanding the scope of this impact is an essential prerequisite to addressing long term conservation management issues in these woods.

Conclusion

The composition of Irish woodland today is a product of past climate change, tree migration abilities and human intervention. However, the current extent of Irish woodland is almost solely a function of human exploitation. This paper has concentrated on examining the past to provide context for today, but this examination also has relevance to the future. Augustine Henry knew what trees would grow well under Irish conditions and he argued for rapidly establishing a national timber resource (Pim 1966). Henry's target of one million acres has now been exceeded as Irish forestry embarks on an exciting future. A wider range of land is now available for planting and there is a greater demand for more diverse species mixes. This is coupled with the much wider recognition of the need for multifunctional forestry. We are fortunate that we can draw on a much wider knowledge base than was available to Henry and we have a greater understanding of forest ecology and succession. So we press forward with wider objectives armed with our substantially improved knowledge but we also have the responsibility that in planning and executing forestry policy in the future we have far less excuses than our predecessors for making mistakes.

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