



Re-defining the natural range of Scots Pine (*Pinus sylvestris* L.): a newly discovered microrefugium in western Ireland

Alwynne H. McGeever^{1*} and Fraser J. G. Mitchell²

¹Trinity Centre for Biodiversity Research and Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland, ²Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

ABSTRACT

Aim Native *Pinus sylvestris* became extirpated in Ireland, during a massive population decline experienced throughout Europe. It was extensively replanted in Ireland during the 18th century from Scottish stock. We test the hypothesis that *P. sylvestris* in Rockforest Co. Clare did not become extirpated during the *P. sylvestris* decline, and persisted to present day independent of 18th century plantations.

Location Rockforest, Co. Clare in Ireland.

Methods Fossil pollen was counted from a terrestrial core. Radiocarbon dates and age-depth modelling was used to ascertain the core chronology. Loss-on-ignition was carried out to investigate sediment accumulation history. Pollen was also counted from moss polster pollen traps to explore the deposition of *P. sylvestris* pollen in the surrounding landscape. Historical maps were consulted to investigate the longevity of other nearby *P. sylvestris* populations.

Results A continuous record of *P. sylvestris* is reported. The core extends through the last two millennia, and reports a clear decline of *P. sylvestris* at c. 1550 cal BP. The *P. sylvestris* pollen curve recovers quickly after the decline event and persists at high levels up until the present day. The loss-on-ignition data reveal a stable accumulation of sediment with no major erosion events. The moss polster pollen traps show the core site is a suitable location for collecting pollen from the Rockforest *P. sylvestris* population. Historical maps demonstrate that none of the other nearby *P. sylvestris* populations extends further back than plantations in the early 18th century.

Main conclusions The population of *P. sylvestris* in Rockforest Co. Clare survived the regional *P. sylvestris* decline, recovered and persisted right up to the present day, independent of introduction by human agency. Hence, we identify this microrefugium population of native Irish stock outside of the current understanding of the native range for this tree species.

Keywords

Ireland, microrefugium, palaeoecology, palaeopalynology, pine decline, *Pinus sylvestris*, Scots Pine

*Correspondence: Alwynne H. McGeever, Trinity Centre for Biodiversity Research and Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland.
E-mail: mcgeevea@tcd.ie

INTRODUCTION

The concept of what constitutes a native species, and its resultant conservation value, has become increasingly relevant due to the recent challenges of biodiversity loss from invasive non-native species (Simberloff *et al.*, 2013) and the call for biodiversity inventories to inform conservation policies (Perrin *et al.*,

2006). *Pinus sylvestris* L. is one of the most widely distributed tree species in the world. It occupies the temperate conifer forest biome in Europe, the distribution of which is between around 40° N, 70° N, 10° W and 70° E (Hultén & Fries, 1986; Cheddadi *et al.*, 2006). *Pinus sylvestris* is the most widespread *Pinus* species, growing successfully throughout much of Eurasia (Rehfeldt *et al.*, 2002). The wide range of this species is proba-

bly due to its broad ecological tolerance (Kelly and Connolly, 2000) and wide climatic range (Cheddadi *et al.*, 2006).

Extirpation of species, mostly mammals, has been recorded in north-west Europe throughout the Holocene. *Pinus sylvestris* stands out as the only significant tree lost during this time. This tree species was widespread during the early to mid-Holocene but became extirpated in Ireland, Wales, England, Denmark, Belgium and the Netherlands (Huntley & Birks, 1983). The non-native status of *P. sylvestris* in these regions has been based on a long history of planting and poor representation in the pollen record. While planting of introduced stock is undisputed, the interpretation of the pollen record can be challenged. This challenge arises from the early idea that *Pinus* presence in pollen records must be above a certain pollen percentage threshold (Bennett, 1984). However, *Pinus* stomata found along with pollen in Scotland provide evidence of indisputable local presence and are often found in association with very low pollen percentages (Froyd, 2005). This implies that small isolated *Pinus* populations could have survived but have been invisible in regional pollen records. We test this assumption in what was the most westerly European outpost of *P. sylvestris*; Ireland.

Pinus sylvestris colonized Britain through south-east England c. 11,470 cal BP [for consistency, radiocarbon dates in the literature were calibrated into cal BP units using OxCAL 4.2 (Bronk Ramsey, 2009) and IntCal13 (Bronk Ramsey, 2013; Reimer *et al.*, 2013)] and spread as far as northern Scotland by 4470 cal BP (Birks, 1989). The Irish population may originate from English stock, or it may have spread independently from a glacial refugium on the continental shelf (Birks, 1989). Evidence for this was found in a site in the south-west of Ireland (Watts, 1984), where *P. sylvestris* was present from 10,740 cal BP, before it was present in the east of Ireland. From 10,200–8350 cal BP, *P. sylvestris* spread throughout Ireland (Mitchell, 2006). Despite its widespread distribution, it was often restricted in the habitats it occurred in due to out-shading on fertile soils by deciduous trees like *Ulmus* and *Quercus*. From 8350 cal BP, the spread of *Alnus glutinosa* significantly restricted the distribution of *P. sylvestris*, particularly in lowland habitats. In the uplands and the western seaboard, the populations of *P. sylvestris* were also reduced by the spread of blanket bog (Bennett, 1984; McGeever & Mitchell, 2015).

A combination of these, and other putative drivers such as climate change, human activity and pathogens, led to a widespread decline in *P. sylvestris* (Roche *et al.*, 2009; McGeever & Mitchell, 2015). This decline was asynchronous in nature affecting populations throughout Europe and *P. sylvestris* became extirpated in England, Wales, Belgium, the Netherlands and Denmark (Bradshaw & Brown, 1987; Birks, 1989; Hannon *et al.*, 2000; Lust *et al.*, 2008). Presently, it is also understood to have become extirpated from Ireland (Bennett, 1984). *Pinus sylvestris* persisted into historic times in several western and upland locations in the Ireland (Bradshaw & Brown, 1987). In Ireland the decline can be divided

into two phases, the first of which was a widespread decline around 4470 cal BP (Roche *et al.*, 2009), where *Pinus* mostly disappeared from the Irish landscape. Small and isolated populations persisted in some locations as evidenced by fine resolution small hollow pollen diagrams in the west and south-west of Ireland (Watts, 1984; Dodson & Bradshaw, 1987; Mitchell, 1988; Jeličić & O'Connell, 1992; Little *et al.*, 1996; Feeser & O'Connell, 2010) where the declines occurred more recently around 1780, 1950, 2150 and 1490 cal BP respectively. This second phase of the decline in isolated populations is also demonstrated in macrofossil evidence such as *Pinus* stumps found in a bog in the Irish midlands (McAulay & Watts, 1961) two stumps in the south-west (Mitchell, 1988) and one stump in Co. Clare (Watts, 1984) dated around 1490, 1740, 1730 and 1055 cal BP respectively. These data represent the second population decline at around 1600 cal BP. This is only about three tree generations until reintroduction in the early 18th century by plantations, most likely from Scottish stock (Roche *et al.*, 2009). Despite this, there are no published data that suggest *Pinus* persisted in Ireland and so this species is classified as non-native in Ireland (Carlisle & Brown, 1968). Of these sites with late native *P. sylvestris* records, only in Rockforest do we find mature *P. sylvestris* in the landscape today with no planting record. Consequently, this site was chosen for this investigation.

Rockforest is located in the karst limestone landscape of western Ireland. The contemporary ecology of this *P. sylvestris* stand is reported in Roche *et al.* (2009). Its vegetation community was described as a *Corylus avellana*–*Brachypodium sylvaticum* association by Roche *et al.* (2009). The ecology of the wider Burren region is noted for its diverse and unusual range of flora, supporting mediterranean, arctic and alpine plants, as well as north continental flora. For further details on the ecology of the Rockforest *P. sylvestris* stand and the wider Burren area, see Roche *et al.* (2009) and Ivimey-Cook & Proctor (1964).

The history of this *P. sylvestris* population has been investigated at a different palaeoecological site (Roche, 2009) which produced a pollen diagram from a nearby lake that extends back 1514 cal BP. The pollen data were quite homogenous in nature, and sampled every 4–8 cm (with a temporal resolution varying from one sample every 50–200 years). Despite this low temporal resolution, and some questions surrounding the sedimentation continuity, the *P. sylvestris* pollen curve appeared to be continuous throughout the core. Hence, these findings justify further investigation into the history of the Rockforest *P. sylvestris* stand.

Clarifying the native status of *P. sylvestris* is of crucial conservation importance. In Ireland *P. sylvestris* has become well established, integrated and is successfully naturalizing in Irish semi-natural habitats (Roche *et al.*, 2009). With only 11% of Ireland's land cover attributed to forest (ITGA, 2012), classifying *P. sylvestris* as a native Irish tree, and identifying the native Irish stock, will have significant consequences for future conservation and re-establishment of native Irish

woodlands. Testing this hypothesis has broader international implications, particularly at the limits of *P. sylvestris*' natural range. It tests the potential for small populations to have persisted locally during a regional decline and demonstrates the potential for our current understanding of modern regional ecology to be expanded through local palaeoecological investigations. It thus provides a contemporary model of a microrefugium (Rull, 2009).

The concept of a native plant was defined as one that has arrived before Neolithic times, or has arrived since without human agency (Webb, 1985). This definition is further refined into three perspectives; boundaries, human agency and time-scale (Kendle & Rose, 2000). In the case of our investigation, the boundary is the island of Ireland, the potential for human agency is the extensive replanting of *P. sylvestris* since the 18th century and the time-scale defines the native Scots Pine as those originating from before the regional *Pinus* decline. As the *P. sylvestris* stand in Rockforest is located within the confines of the Irish island, two criteria remain to be satisfied to prove it is native: firstly that it originates from before the 18th century reintroduction, and secondly that it survived the *Pinus* decline, which occurred in this region of Ireland around 1600 cal BP. The evidence to demonstrate that these criteria are met would be found in a continuous record of relatively high *Pinus* pollen percentages over time, particularly between the time of the regional *Pinus* decline and 18th century plantations, when *P. sylvestris* was presumed extirpated in Ireland.

This paper sets out to test the hypothesis that *P. sylvestris* in Rockforest Co. Clare did not become extirpated during the *Pinus* decline, and persisted to the present day independent of 18th century plantations. This was tested by carrying out a high resolution pollen analysis from a new location in the Rockforest area.

MATERIALS AND METHODS

The site chosen for this study lies on one of the most western outposts of Europe and so, also the most western potential ecological range of *P. sylvestris*. The Burren is a region of karstified Carboniferous limestone pavement in the west of Ireland, where there is a mild oceanic climate. The site lies on the eastern margin of the Burren Plateau (Fig. 1).

Numerous small lakes occur in a karst landscape surrounding the Rockforest *P. sylvestris* population but surveying revealed that sediment did not accumulate in these lakes. Consequently, a core was extracted from Aughrim swamp c. 100 × 40 m in size that was hydrologically linked to Rockforest Lough. The sediment core described by Roche (2009) was extracted directly from the western part of Rockforest Lough, some 0.85 km south-west of Aughrim swamp selected for the current investigation. The site occurred at an elevation of 40 m OD at latitude 53.01 and longitude -8.95 (Fig. 1). The core was taken from the centre of the swamp, with a water depth of 44 cm, where the peat was at its deepest. The core was extracted using a Wardenaar corer

(Wardenaar, 1987), wrapped in polythene film and tinfoil and stored at 4 °C.

The core was divided longitudinally, and one half stored as a backup record. The remaining half was described using the Troels-Smith sediment description scheme (Troels-Smith, 1955). Pollen was extracted at 1 cm intervals using standard preparation techniques (Faegri *et al.*, 1989). Towards the base of the core the sediment graded from peat to clay, and dense-media separation techniques were used to remove the inorganic sediment (Nakagawa *et al.*, 1998).

Pollen

A minimum of 300 pollen grains were counted per level. Pollen was identified using ×400 magnification. For pollen identification, reference was made to a pollen reference collection and identification keys (Moore *et al.*, 1991; Reille, 1995; Beug, 2004). The pollen sum was calculated using the terrestrial pollen sum, excluding local aquatic taxa. Standard pollen nomenclature was followed (Moore *et al.*, 1991), where applicable taxonomic names were updated using the standardized taxa lookup files of TILIA 2 and the Neotoma database (Grimm, 2013). TILIA 2 (Grimm, 2013) was used to calculate the pollen percentages and draw a pollen diagram of the key taxa, with loss-of-ignition and sediment description results.

Chronology

The core was 75 cm in length, with pollen investigated to a depth of 55 cm. For dating, bulk sediment samples of 5 cm³ were extracted from 20 and 48 cm in the core. The sample at 48 cm was taken at the point of a prominent decline in the percentage of *Pinus* pollen, representing the population decline event. The material was passed through a coarse sieve to remove potential contamination from the modern root material. The sieved sediment was dried in an oven at 60 °C, and then sent to Beta Analytic for AMS Radiocarbon dating. The R package BChron 4 (Haslett & Parnell, 2008) was used to establish a chronology for the core, using the two bulk sample radiocarbon dates. The radiocarbon date for the *Pinus* decline was calibrated using OxCal 4.2 and IntCal13 (Bronk Ramsey, 2009, 2013; Reimer *et al.*, 2013) and compared to the radiocarbon date of four other published *P. sylvestris* decline radiocarbon dates in the south-west of Ireland.

Loss-on-ignition

Loss-on-ignition was carried out at 1 cm intervals throughout the core, to investigate the sedimentological history of the site. Around 3 cm³ of sediment was extracted from contiguous 1 cm depths of the core. The samples were dried overnight at 60 °C and weighed. The samples were then ignited at 550 °C for 5 h and re-weighed to obtain an estimate of the organic matter content. The samples were again ignited for a further 3 h at 950 °C to estimate the carbonate and mineral content.

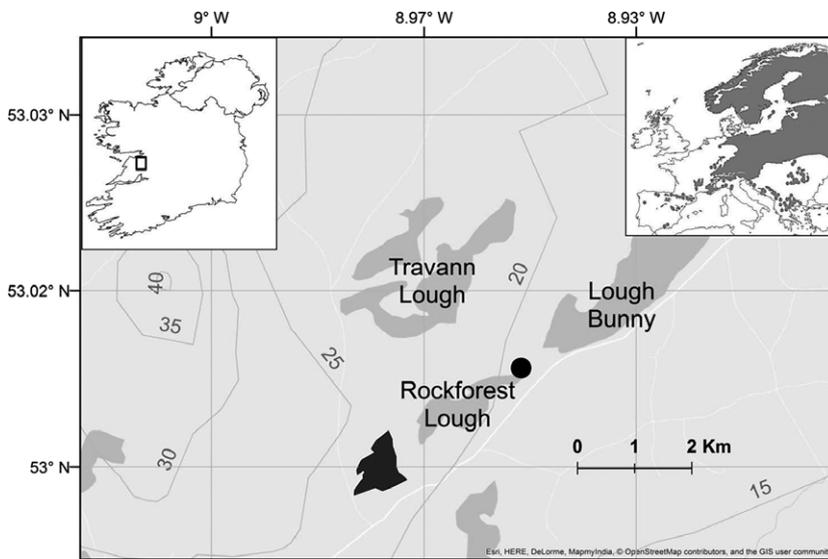


Figure 1 Location of core site in Aughrim Swamp in Co. Clare, Ireland, with inset map of Europe showing *Pinus sylvestris* distribution in grey (From: EURFORGEN, 2009) and Ireland. Dark Grey shading: Rockforest *P. sylvestris* stand. Grey lines: elevation contours. White lines: roads.

Moss polsters

Modern pollen rain was investigated through the analysis of moss polsters which were collected from six sites around the existing population of *P. sylvestris* in Rockforest. This was done to gain insight into the distribution of *P. sylvestris* pollen on the landscape surrounding the putative native stand, and the core site. Approximately 100 mL of moss was placed in a conical flask of distilled water for each sample. The samples were shaken for 45 min. The moss and water was then transferred through a sieve into centrifuge tubes. The samples were centrifuged at 1465 g for 5 min to extract pollen and sediment from the solution. The supernatant was decanted and the standard pollen preparation was applied to the resultant sample (Faegri *et al.*, 1989). Pollen was counted at $\times 400$ magnification on a light microscope, to a count of 300 grains per sample.

Historical maps

Satellite images and maps were used to identify any other areas of forestry, besides Rockforest, within an 8 km radius of the core site. The historical maps database (Clare County Library, 2015) and Ordnance Survey Ireland (OSI, 2015) were used to survey the area around the core site. Over 100 maps of Co. Clare were searched, dating from 1653 until present day. However, the historic Ordnance survey map of 1842 was the earliest to provide details on land use. Hence, the maps used to reconstruct historic forestry distribution within an 8 km radius of the core site included the 1842 Ordnance survey, and the Ordnance survey satellite images of 1995, 2000 and 2005.

RESULTS

The core was 75 cm in depth, with good pollen preservation to a depth of 55 cm. The sediment was composed primarily

of peat, with clay and marl material at the base. Four distinct zones were identified and described using the Troels-Smith sediment description scheme (see Appendix S1).

Pollen

Pollen was well preserved to a depth of 55 cm. In total, 73 taxa were identified and *Pinus* was the dominant tree taxon. A prominent decline in *Pinus* can be seen at 48 cm, although it quickly recovers to sustained levels above the present day values (Fig. 2).

Chronology

The two sediment samples taken at 20 cm (Beta-395999) and 48 cm (Beta-396000) were dated to 1120 ± 30 BP (around 1020 cal BP) and 1650 ± 30 BP (around 1550 cal BP) respectively (Fig. 3). The record extends as far back as 1600 cal BP.

The date of the Rockforest *Pinus* decline was compared with published dates from four other sites in the south-west region of Ireland. These dates were from stumps in the south-west (Co. Kerry) radiocarbon dated around 1740 and 1730 cal BP (Mitchell, 1988), sites in Co. Clare report the *Pinus* decline around 2150 cal BP (Feeser & O'Connell, 2010) and 1490 cal BP (Jeličić & O'Connell, 1992). A stump from the Burren region in Co. Clare was radiocarbon dated around 1050 cal BP (Watts, 1984). The calibrated date of the Rockforest *Pinus* decline was around 1550 cal BP 95.4% range, OxCAL 4.2 (Bronk Ramsey, 2009, 2013) and IntCal13 (Reimer *et al.*, 2013). This calibrated date lies within the calibrated ranges of the other *Pinus* declines in the region (Fig. 4).

Loss-on-ignition

The results for the loss-on-ignition can be seen in Fig. 2. The mean mineral content was 34.1%. Overall there is a very

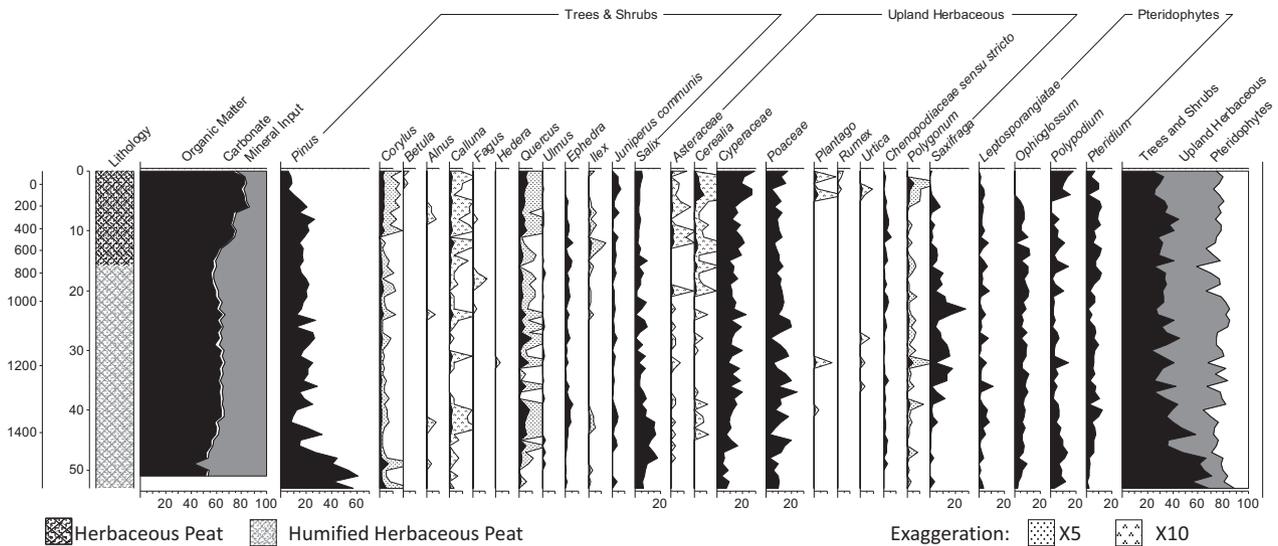


Figure 2 Percentage pollen diagram of principal taxa for pollen of core from Aughrim Swamp, the Burren, Co. Clare, Ireland.

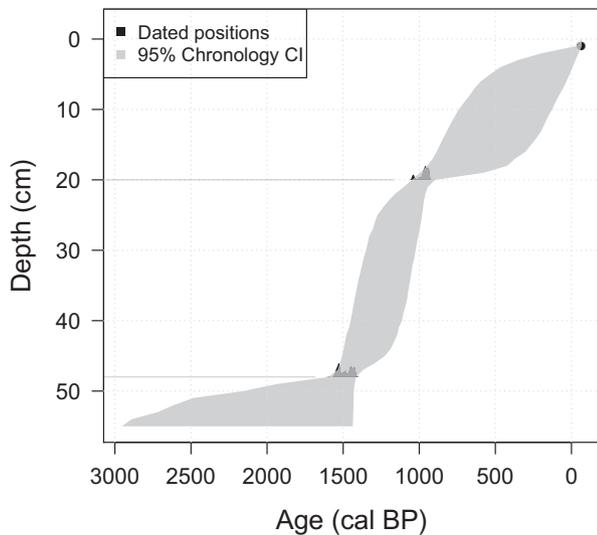


Figure 3 Age-Depth chronology of Aughrim Swamp core, Ireland, using radiocarbon dates Beta-395999 and Beta-396000. Constructed using R package Bchron 4 (Haslett & Parnell, 2008).

low carbonate content, with an average percentage of 1.96%. The organic matter is highest at the top of the core and decreases gradually from 11–16 cm. The mineral content stays at relatively stable levels from 16–49 cm. There is a sharp increase in mineral content at from 49–50 cm, which recovers at 51 cm (Fig. 2).

Moss polsters

The percentage of *Pinus* pollen is highest from the moss polster taken from under the forest canopy (Polster 5, Fig. 5, see Appendix S3). The *Pinus* pollen percentage of the surface sample of the site core is higher than most of the moss polsters, surpassed only by the forest sample (Polster 5) and

Polster 1. Polster 5 has notably more *Corylus* pollen than the other samples.

Historical maps

Eleven other forestry ‘parcels’ were identified within the 8 km radius of the core using satellite images (see Appendix S2). These ranged from 0.4 to 67.1 ha in area, and occurred from 3.5 to 8.0 km from the core site. Historical maps were used to identify when these forests developed on the landscape. Ten of the 11 forestry parcels developed within the last 235 years (see Appendix S2).

One forest parcel extends back beyond the map records (Forest 2; see Appendix S2). This forest occurs in the area of Derryowen, which might be translated to ‘Owen’s Oakwood’ (Burke, 2009). It occupies a very small area of only 2.4 ha and lies 5.5 km south-east of the core site. The symbols on the 1842 map indicate it was a mixed broadleaf and coniferous wood. The ruins of a castle lies within 200 m of the forest that dates back to the 15th century, with a reference to a wood in the area in 1598 (O’Donovan & Curry, 1839). It is difficult to determine whether this references this particular piece of woodland. However, within the forested land of the 1842 map is Derryowen house, which was part of the Lopdell estate in the 19th century. A notice announcing the sale of this house in July 1889 describes it as ‘a very good newly built dwelling-house, with suitable out-offices’ (MooreInstitute, 2015). This would suggest the house was built at some point in the 19th century, and so it is likely the trees were planted at some point in the early 1800s.

DISCUSSION

The findings of this work support the hypothesis that *P. sylvestris* in Rockforest Co. Clare did not become extirpated during the *P. sylvestris* decline, and persisted to

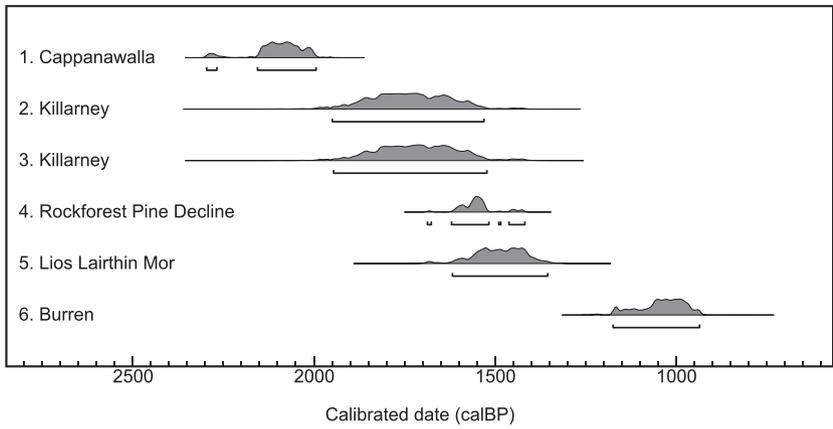


Figure 4 Calibrated radiocarbon dates of pine declines in the south-west of Ireland (OxCal 4.2 and IntCal13; Bronk Ramsey, 2009, 2013). 1. Feeser and O’Connell (2010), 2 and 3. Mitchell (1988), 4. Putative native Rockforest site, 5. Jeličić & O’Connell (1992), 6. Watts (1984).

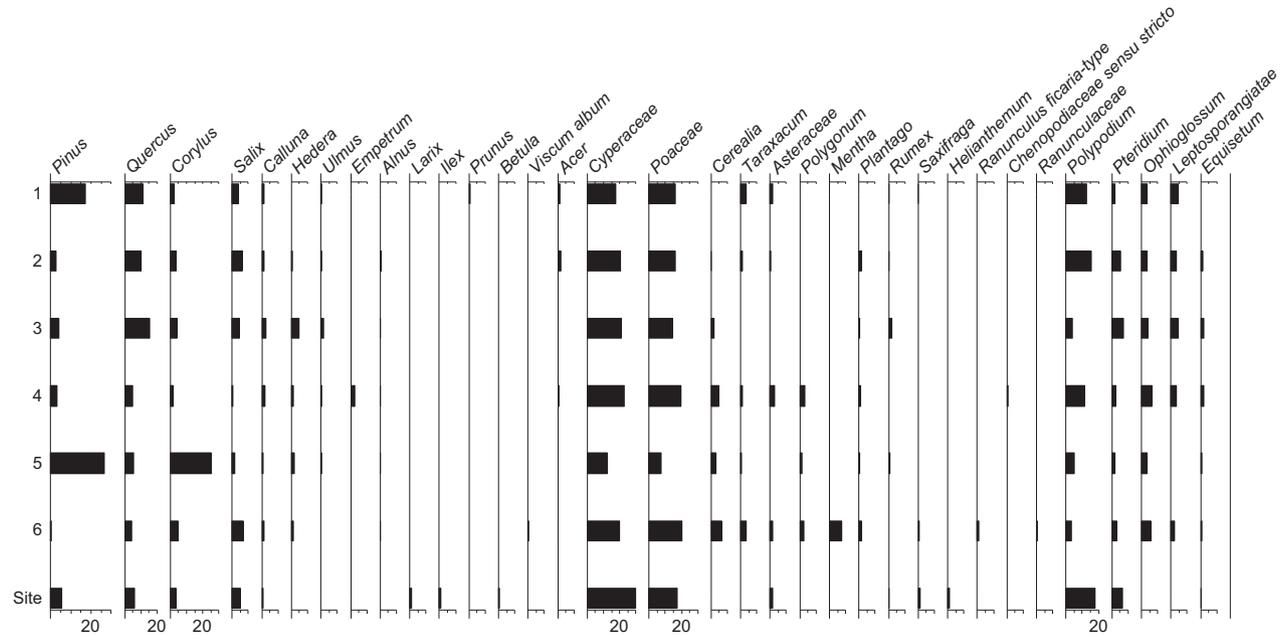


Figure 5 Percentage pollen data for six moss polster pollen traps and the first cm of the Aughrim Swamp core, Ireland.

present day independent of 18th century plantations. Hence, we consider there to be sufficient evidence for *P. sylvestris* to be classified as a native Irish tree. Unlike previous investigations (Roche, 2009), this pollen diagram does show a distinct *P. sylvestris* decline at c. 48 cm. However, atypical of traditional *Pinus* pollen curves in Irish pollen diagrams (Buzer, 1980; Mitchell, 1990; O’Connell & Molloy, 2001; O’Connell *et al.*, 2001), this *Pinus* curve recovers relatively soon after the *Pinus* decline. The Aughrim Swamp LOI results are relatively continuous throughout (Fig. 2), supporting the integrity of this core sequence with no major hiatus. A sudden change in the ratio of mineral to organic content would suggest the occurrence of an erosion event (Bradshaw & McGee, 1988; Stevenson *et al.*, 1990; Evans & Warburton, 2011). The continuous nature of the loss-on-ignition and pollen records shows no reason to suspect the sediment accumulation was not continuous and uninterrupted since the decline event, supporting the integrity of the core chronology.

When was Scots Pine present?

At the top of the core, the *Pinus* pollen per cent is c. 5% of the total pollen sum, at a time when we know there is a definite presence of *P. sylvestris* in the area today. Since the *Pinus* decline around 1550 cal BP, the *Pinus* pollen has maintained percentage values above this threshold. There has been much debate over what pollen percentage should indicate a *P. sylvestris* presence. *Pinus* pollen can easily travel long distances, with two air bladders facilitating dispersal (Pessi & Pulkkinen, 1994). Originally a ‘critical pollen percentage’ of 20% was suggested to indicate a *P. sylvestris* presence (Bennett, 1984). This was later revised to 5% (Bennett, 1995). However, others have demonstrated a *P. sylvestris* presence with values lower than 5% using stomata to indicate an indisputable presence. Examples of these can be seen elsewhere Ireland, where *P. sylvestris* presence was found with pollen values as low as 2.8% (Fossitt, 1994) and 2.3%

(Cooney, 1996) and in Scotland *P. sylvestris* was proven to occur when pollen was only 0.4% (Froyd, 2005). The dynamics of pollen dispersal are complex and difficult to reliably predict. In the case of this investigation there are several considerations that might justify using a *Pinus* pollen value of 5% to indicate a native presence. Firstly, at the top of the core the *Pinus* pollen percentage fluctuates around the 5% mark, at a time when we know *P. sylvestris* to be present from the contemporary Rockforest population. This is further supported by an investigation of contemporary pollen deposition in the area around the coring site and Rockforest using moss polsters as pollen traps (Fig. 5). Secondly, the location of the site in the west of Ireland significantly minimizes the likelihood of the *Pinus* pollen coming from another country, and so we conclude that the *Pinus* pollen must be from Irish populations. And thirdly, it is unlikely that pollen from further away would have been deposited and preserved at this site due to the size of the basin (40 × 100 m); smaller basins tend to represent local pollen sources compared to larger basins which show more regional vegetation dynamics (Sugita, 2007).

The timing of the *Pinus* decline at Rockforest

Other pollen sites in this region of Ireland also show a distinct *P. sylvestris* decline, but with no recovery (Watts, 1984; Jeličić & O'Connell, 1992; Feaser & O'Connell, 2010). The most likely reason for our site detecting a *P. sylvestris* recovery while other sites did not is its proximity to the putative native stand. Some nearby sites show 'smearing' in the *Pinus* pollen curve after the *P. sylvestris* decline (Watts, 1984), which might be representing the persisting Rockforest population. Our core shows the *Pinus* decline to have occurred at 48 cm, around 1550 cal BP. In western and upland areas of Ireland, *Pinus* persisted into historic times (Bradshaw & Browne, 1987). The decline was similarly timed in other sites in Ireland (McAulay & Watts, 1961; Watts, 1984; Dodson & Bradshaw, 1987; Mitchell, 1988; Feaser & O'Connell, 2010). The date of the Rockforest *Pinus* decline is consistent with other declines in this area of Ireland (Fig. 4).

Pinus pollen in the area around the Aughrim Swamp core

Moss polsters were successfully collected and analysed as modern pollen traps. These were used to provide insight into the distribution of *Pinus* pollen around the Rockforest stand of *P. sylvestris*. Olalla *et al.* (1994) found four mechanisms that influence the distribution of pollen on the landscape: topography, distance from pollen source, local vegetation composition and wind turbulence. The area of Rockforest is relatively flat topographically, but all the other factors are likely influencers of the moss polster results. These modern pollen traps show that the sample taken closest to the pollen source has the highest representation of *Pinus* pollen (Polster 5, Fig. 5, see Appendix S3). Counter intuitively, Polster 1 has quite

high representation of *Pinus* pollen (Fig. 5), despite it being one of the furthest away from the Rockforest *P. sylvestris* stand (2.5 km, see Appendix S3). This pollen trap was taken from an open area of karst landscape. It is possible that the sparse local vegetation cover at the polster site contributed to the high representation of *Pinus* pollen. The remaining polsters have much lower percentage of *Pinus* pollen related to their distance from the stand and dilution with pollen from other taxa. The *Pinus*:Poaceae ratio is 1.04 and 3.66 for Polsters 1 and 5 respectively compared to < 0.3 for Polsters 2, 3, 4 and 6 (Fig. 5, see Appendix S3).

Pinus sylvestris stands in the area around the Rockforest stand

Historical maps were consulted to provide additional context into the distribution of *P. sylvestris* in the wider landscape. An 8 km radius was chosen because the core site itself lies in a small basin of only 40 × 100 m in area. Small basins represent pollen from a local area (Sugita, 2007), so an 8 km radius is a conservatively large area to survey for *P. sylvestris* populations relevant to the area being surveyed in a palaeoecological context by the core.

A review of historical maps successfully provided records of forest plantations, that likely would include *P. sylvestris*, representing the re-introduction of this species to the area (see Appendix S2). This is consistent with the current narrative for this species in Ireland; being reintroduced by anthropogenic agency since the early 18th century (Roche *et al.*, 2009).

Why did *P. sylvestris* survive in Rockforest?

This is the first Irish *P. sylvestris* population to be found that has survived since before the population decline and 'extirpation' event. At this point the reason for it surviving can only be discussed speculatively. It is very possible that future palaeoecological investigations may find similar populations and more insight might be gained into why these stands survived. What is clear from this work, is that whatever caused *P. sylvestris* to decline had an impact on the population in Rockforest; the population did decline, but recovered. Therefore, the possibility of the population simply being too geographically isolated to experience the decline can be dismissed. The main causal mechanisms suggested for the decline of *P. sylvestris* in Ireland are (1) being out-competed by *Alnus glutinosa* and (2) habitat loss to blanket bogs (3) human exploitation (Bennett, 1984; Roche *et al.*, 2009; McGeever & Mitchell, 2015).

Human exploitation is likely to have been the principal causal mechanism for the final historic decline in *P. sylvestris* in Ireland. Human exploitation of the Irish landscape has been ongoing for millennia (Mitchell & Ryan, 1997). *Pinus sylvestris* was particularly vulnerable because unlike most other Irish trees it does not naturally coppice and the root stock dies following felling. Almost all semi-natural forest in Ireland has survived through virtue of being located within estates that were established from c. 12th century through to

the 18th century (Rackham, 1995). This afforded some protection and reduced the risk of forest being converted to farmland. In the case of Rockforest *P. sylvestris* stand lies within the Rockforest estate. The trees grow on limestone pavement which would have been unattractive to convert to agricultural land and we thus assume that the estate ownership protected the trees from felling for timber.

Wider relevance of this study

Our study uses fossil evidence to elucidate new features in the population dynamics of *P. sylvestris* in Ireland, which has much wider implications for the regional dynamics of this species. Another example of the use of fossil evidence can be seen in the work of De Nascimento *et al.* (2009), who show the impact of anthropogenic disturbance on forest ecosystems in Tenerife. The past dynamics of plant populations can be further elucidated when fossil evidence is coupled with distribution models. For example, Bialozyt *et al.* (2012) use a model of the dispersal characteristics of *Fagus sylvatica* and *Picea abies* to gain new insight into their history in Scandinavia. Similarly Manning *et al.* (2010) use bioclimatic modelling to identify areas in northern England and southern Scotland that *P. sylvestris* may have survived, narrowing the ongoing search for refugia populations there.

With the accumulation of historical data on plant distributions from fossil records, species distributional models and phylogeographical surveys, the search for plant refugial populations is becoming increasingly successful. Finding refugial populations is important due to their crucial role in the maintenance of regional biodiversity over long time periods (Gavin *et al.*, 2014). Our work here compliments and contributes to the wider use of approaches employed in the search for refugia, and demonstrate a successful discovery of a refugial population using a palaeoecological approach. Future research may employ species distributional models and phylogeographical studies to identify other potentially native stands of *P. sylvestris* in Ireland, which can then be confirmed by a palaeoecological study.

CONCLUSION

Our investigation demonstrated the potential for palaeoecology to contribute to our understanding of modern ecology. We demonstrate that *P. sylvestris* deserves reclassification of its status and to be re-established as a native Irish tree. It has maintained a continuous Irish presence despite its declines. We identify the population in Rockforest, Co. Clare to be of native Irish stock and hence of significant genetic provenance, as so far, other Irish *P. sylvestris* populations are believed to have resulted from human introductions during the 18th century. Evidence for these findings have been found in the radiocarbon dated palynological record, interrogating the sediment accumulation constancy using loss-on-ignition, investigating the pollen distribution in the surrounding landscape using moss pollen traps, and exploring the forest history in the area through historical maps. We find the core to be of a

sufficient age to include the *Pinus* decline, with no major disruptions to the accumulation of sediment, in a location that is ideal for collecting *Pinus* pollen from the Rockforest population. We are also confident that the decline dated around 1550 cal BP is the population decline found elsewhere in Ireland, as this date is consistent with the timing of the decline event at other sites in this region. Hence, we identify a microrefugium for *P. sylvestris* in this region of Europe originating from before the regional population decline.

The relevance of these findings is threefold; firstly, this has significant implications for the conservation of Irish flora and further contributes to the already significant conservation value of the Burren Co. Clare, as its unique environment supports the only confirmed native stand of Irish Scots Pine (*P. sylvestris*). Secondly, in a European context it extends the native range of *P. sylvestris* and highlights a realistic potential for native stands of *P. sylvestris* to exist in other regions where it is currently understood to have been extirpated; England, Wales, Denmark, Belgium and The Netherlands. And thirdly, in a palaeoecological context this result is relevant to the interpretations of existing and future *Pinus* pollen records, demonstrating the risk of drawing regional conclusions in the absence of fine resolution local investigations.

ACKNOWLEDGEMENTS

This work was funded by the Trinity Centre for Biodiversity Research and is part of the Earth and Natural Sciences Doctoral Studies Programme. The help during fieldwork from Angela Stevenson, Donna Hawthorne and Emma Glanville was greatly appreciated. We are also particularly grateful to Paddy O'Brien for access to the coring site and to the National Parks and Wildlife Service for access to Rockforest. We also thank Jenni Roche for access to her data and advice on Rockforest. We thank Dr. Rubiales and anonymous referees for their comments on the manuscript.

REFERENCES

- Bennett, K.D. (1984) The post-glacial history of *Pinus sylvestris* in the British Isles. *Quaternary Science Reviews*, **3**, 133–155.
- Bennett, K.D. (1995) Post-glacial dynamics of *Pinus* (*Pinus sylvestris* L.) and *Pinus* woods in Scotland. *Our Pinus wood heritage* (ed. by J.R. Aldhous), pp. 23–29. Forestry Commission, The Royal Society for the Protection of Birds, Scottish Natural Heritage, Farnham.
- Beug, H.J. (2004) *Leitfaden der pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Dr. Friedrich Pfeil, München.
- Bialozyt, R., Bradley, L.R. & Bradshaw, R.H. (2012) Modelling the spread of *Fagus sylvatica* and *Picea abies* in southern Scandinavia during the late Holocene. *Journal of Biogeography*, **39**, 665–675.
- Birks, H.J. (1989) Holocene isochrone maps and patterns of tree-spreading in the British Isles. *Journal of Biogeography*, **16**, 503–540.

- Bradshaw, R. & McGee, E. (1988) The extent and time-course of mountain blanket peat erosion in Ireland. *New Phytologist*, **108**, 219–224.
- Bradshaw, R.H.W. & Browne, P. (1987) Changing patterns in the post-glacial distribution of *Pinus sylvestris* in Ireland. *Journal of Biogeography*, **14**, 237–248.
- Bronk Ramsey, C. (2009) Bayesian analysis of radiocarbon dates. *Radiocarbon*, **51**, 337–360.
- Bronk Ramsey, C. (2013) *OxCal Program, version 4.2*. Available at: <http://c14.arch.ox.ac.uk/oxcal.html>. Radiocarbon Accelerator Unit, University of Oxford.
- Burke, A. (2009) The Derryhivenny castle project. *Group for the Study of Irish Historic Settlement*, **14**, 21–26.
- Buzer, J.S. (1980) Pollen analyses of sediments from Lough Ine and Ballyally Lough, Co., Cork, S.W. Ireland. *New Phytologist*, **86**, 93–108.
- Carlisle, A. & Brown, A.H.F. (1968) *Pinus sylvestris* L. *Journal of Ecology*, **56**, 269–307.
- Cheddadi, R., Vendramin, G.G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J.M., De Beaulieu, J.L., Sadori, L., Jost, A. & Lunt, D. (2006) Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Global Ecology and Biogeography*, **15**, 271–282.
- Clare County Library (2015) *Historical maps of County Clare*. Available at: www.clarelibrary.ie (accessed 8 January 2015).
- Cooney, T. (1996) Vegetation changes associated with late-neolithic copper mining in Killarney. *Central Kerry. Field Guide* (ed. by C. Delaney and P. Coxon). Irish Association for Quaternary Studies, Dublin.
- De Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C. & Whittaker, R.J. (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography*, **36**, 499–514.
- Dodson, J.R. & Bradshaw, R.H.W. (1987) A history of vegetation and fire, 6600 Bp to present, County Sligo, Western Ireland. *Boreas*, **16**, 113–123.
- EURFORGEN (2009) *Distribution map of Scots Pine (Pinus sylvestris)*. Available at: www.euforgen.org (accessed 6 November 2015).
- Evans, M. & Warburton, J. (2011) *Geomorphology of upland peat: erosion, form and landscape change*. Wiley & Sons Ltd, Chichester.
- Fægri, K., Kaland, P.E. & Krzywinski, K. (1989) *Textbook of pollen analysis*. Wiley & Sons Ltd, Chichester.
- Feeser, I. & O'Connell, M. (2010) Late Holocene land-use and vegetation dynamics in an upland karst region based on pollen and coprophilous fungal spore analyses: an example from the Burren, western Ireland. *Vegetation History and Archaeobotany*, **19**, 409–426.
- Fossitt, J. (1994) Late-glacial and Holocene vegetation history of western Donegal, Ireland. *Biology and Environment*, **94B**, 1–31.
- Froyd, C. (2005) Fossil stomata reveal early pine presence in Scotland: implications for postglacial colonization analyses. *Ecology*, **86**, 579–586.
- Gavin, D.G., Fitzpatrick, M.C., Gugger, P.F., Heath, K.D., Rodríguez-Sánchez, F., Dobrowski, S.Z., Hampe, A., Hu, F.S., Ashcroft, M.B. & Bartlein, P.J. (2014) Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytologist*, **204**, 37–54.
- Grimm, E. (2013) *Tilia and TGview software*. Illinois State Museum, Springfield, IL.
- Hannon, G.E., Bradshaw, R. & Emborg, J. (2000) 6000 years of forest dynamics in Suserup Skov, a seminatural Danish woodland. *Global Ecology and Biogeography*, **9**, 101–114.
- Haslett, J. & Parnell, A. (2008) A simple monotone process with application to radiocarbon-dated depth chronologies. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, **57**, 399–418.
- Hultén, E. & Fries, M. (1986) *Atlas of North European vascular plants (North of the Tropic of Cancer)*, Vols I–III. Koeltz Scientific Books, Königstein.
- Huntley, B. & Birks, H.J.B. (1983) *Atlas of past and present pollen maps for Europe, 0–13,000 years ago*. Cambridge University Press, Cambridge.
- ITGA (2012) *Forestry and timber yearbook 2012*. Irish Timber Growers Association, Dublin.
- Ivimey-Cook, R.B. & Proctor, M.C.F. (1964) The plant communities of the Burren, Co., Clare. *Proceedings of the Royal Irish Academy*, **64**, 211–302.
- Jeličić, L. & O'Connell, M. (1992) History of vegetation and land use from 3200 BP to the present in the north-west Burren, a karstic region of western Ireland. *Vegetation History and Archaeobotany*, **1**, 119–140.
- Kelly, D. & Connolly, A. (2000) A review of the plant communities associated with Scots pine (*Pinus sylvestris* L.) in Europe, and an evaluation of putative indicator/specialist species. *Forest Systems*, **9**, 15–39.
- Kendle, A.D. & Rose, J.E. (2000) The aliens have landed! What are the justifications for 'native only' policies in landscape plantings? *Landscape and Urban Planning*, **47**, 19–31.
- Little, D.J., Mitchell, F.J.G., vonEngelbrechten, S. & Farrell, E.P. (1996) Assessment of the impact of past disturbance and prehistoric *Pinus sylvestris* on vegetation dynamics and soil development in Uragh Wood, SW Ireland. *Holocene*, **6**, 90–99.
- Lust, N., Geudens, G. & Olsthoorn, A. (2008) Scots pine in Belgium and the Netherlands. *Forest Systems*, **9**, 213–231.
- Manning, A.D., Kesteven, J., Stein, J., Lunn, A., Xu, T. & Rayner, B. (2010) Could native Scots pines (*Pinus sylvestris*) still persist in northern England and southern Scotland? *Plant Ecology & Diversity*, **3**, 187–201.
- McAulay, I. & Watts, W. (1961) Dublin radiocarbon dates I. *Radiocarbon*, **3**, 26–38.
- McGeever, A.H. & Mitchell, F.J. (2015) Pine stumps in Irish peats: is their occurrence a valid proxy climate indicator? *Journal of Quaternary Science*, **30**, 489–496.
- Mitchell, F.J.G. (1988) The vegetational history of the Killarney oakwoods, SW Ireland: evidence from fine spatial resolution pollen analysis. *Journal of Ecology*, **76**, 415–436.

- Mitchell, F.J.G. (1990) The history and vegetation dynamics of a yew wood (*Taxus baccata* L.) in SW Ireland. *New Phytologist*, **115**, 573–577.
- Mitchell, F.J.G. (2006) Where did Ireland's trees come from? *Biology and Environment*, **106B**, 251–259.
- Mitchell, G.F. & Ryan, M. (1997) *Reading the Irish landscape*. Townhouse, Dublin.
- Moore, P.D., Webb, J.A. & Collison, M.E. (1991) *Pollen analysis*. Blackwell Scientific Publications, Oxford.
- Nakagawa, T., Brugiapaglia, E., Digerfeldt, G., Reille, M., De Beaulieu, J. & Yasuda, Y. (1998) Dense-media separation as a more efficient pollen extraction method for use with organic sediment/deposit samples: comparison with the conventional method. *Boreas*, **27**, 15–24.
- O'Connell, M. & Molloy, K. (2001) Farming and woodland dynamics in Ireland during the Neolithic. *Biology and Environment*, **101B**, 99–128.
- O'Connell, M., Molloy, K. & McMahon, H. (2001) Reconstructing prehistoric farming activity and human impact at a fine spatial resolution: palaeoecological investigations at Mooghaun, Co. Clare, western Ireland. *Beiträge zur Siedlungsarchäologie und zum Landschaftswandel* (ed. by P. Schauer), pp. 161–186. Regensburger Beiträge zur Prähistorischen Archäologie.
- O'Donovan, J. & Curry, E. (1839) *Ordnance survey letters*. Clare County Library, Clare, Ireland.
- Olalla, A.A., Valdeolmillos, A. & Zapata, B.R. (1994) Modern pollen spectra and contemporary vegetation in the Paramera Mountain range (Ávila, Spain). *Review of Palaeobotany and Palynology*, **82**, 129–139.
- OSI (2015) *Explore Map*. Available at: www.osi.ie (accessed 8 January 2015).
- Perrin, P.M., Martin, J.R., Barron, S.J. & Roche, J.R. (2006) A cluster analysis approach to classifying Irish native woodlands. *Biology and Environment*, **106B**, 261–275.
- Pessi, A.-M. & Pulkkinen, P. (1994) Temporal and spatial variation of airborne Scots pine (*Pinus sylvestris*) pollen. *Grana*, **33**, 151–157.
- Rackham, O. (1995) Looking for ancient woodland in Ireland. *Wood, trees and forest in Ireland* (ed. by J.R. Pilcher and S.S. Mac an tSaoir), pp. 1–12. Royal Irish Academy, Dublin.
- Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. & Milyutin, L.I. (2002) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology*, **8**, 912–929.
- Reille, M. (1995) *Pollen et spores d'Europe et d'Afrique du Nord: supplément 1*. Laboratoire de Botanique Historique et Palynologie, Marseille.
- Reimer, P.J., Bard, E., Bayliss, A. et al. (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, **55**, 1869–1887.
- Roche, J. (2009) *Ecology and native status of Scots Pine (Pinus sylvestris L.) in Ireland*. PhD Thesis, University of Dublin Trinity College, Dublin.
- Roche, J.R., Mitchell, F.J.G. & Waldren, S. (2009) Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland. *Biodiversity and Conservation*, **18**, 2185–2203.
- Rull, V. (2009) Microrefugia. *Journal of Biogeography*, **36**, 481–484.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E. & Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution*, **28**, 58–66.
- Stevenson, A., Jones, V. & Battarbee, R. (1990) The cause of peat erosion: a palaeolimnological approach. *New Phytologist*, **114**, 727–735.
- Sugita, S. (2007) Theory of quantitative reconstruction of vegetation II: all you need is LOVE. *The Holocene*, **17**, 243–257.
- Troels-Smith, J. (1955) Karakterisering af løse jordarter [Characterization of unconsolidated sediments]. *Danmarks Geologiske Undersøgelse*, **4**, 73.
- Wardenaar, E. (1987) A new hand tool for cutting peat profiles. *Canadian Journal of Botany*, **65**, 1772–1773.
- Watts, W. (1984) The Holocene vegetation of the Burren, western Ireland. *Lake sediments and environmental history* (ed. by E.Y. Haworth and J.W.G. Lund), pp. 359–376. Leicester University Press, Leicester.
- Webb, D. (1985) What are the criteria for presuming native status? *Watsonia*, **15**, 231–236.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Sediment description.

Appendix S2 List of nearby forest parcels.

Appendix S3 Location of moss polsters.

BIOSKETCHES

Alwynne Hannah McGeever's research interests are in palaeoecology of forest systems, most particularly the dynamics of tree populations in Europe over the last c. 10,000 years, as well as investigating the native status of *Pinus sylvestris* in Ireland and the past dynamics of bog pine woodlands.

Fraser John Gray Mitchell's research interest are in long-term environmental change as well as contemporary ecosystems. This has included investigating the impacts of human activity, grazing and climate on temperate forest succession and the drivers of contemporary forest biodiversity as well as investigation of long-term climate impacts on peatland ecosystems.

Editor: Ole Vetaas