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Article Early to Mid-Holocene Tree Immigration and Spread in the Isle of Man: The Roles of Climate and Other Factors

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Abstract: The Isle of Man is a large island which lies in the middle of the northern Irish Sea between Britain and Ireland and, because of its insularity and size, has an impoverished flora compared with the two main islands. This has been the case throughout the postglacial and warrants the island's description as a separate phytogeographic province. We have considered Holocene tree pollen data from seventeen sites on the island which together preserve a vegetation history that spans the six thousand years of the early and mid-postglacial from the end of the Lateglacial at 11,700 cal. BP to the mid-Holocene Ulmus decline at ca. 5800 cal. BP. Radiocarbon dating of the rational limits of the pollen curves for the main tree taxa has allowed an appraisal of the timing of each one's expansion to become a significant component of the island's woodland, and comparison with the dates of their expansion on the adjacent regions of Britain and Ireland. The radiocarbon dates show that, although some variability exists probably due to local factors, there is considerable concordance between the timings of major pollen zone boundaries in Britain and Ireland around the northern Irish Sea. On the Isle of Man the expansions of both Juniperus and Betula were delayed by several centuries compared to the British/Irish data, however the timing of the expansions of Corylus, Ulmus, Quercus, Pinus and Alnus on the Isle of Man all appear closely comparable to the ages for these pollen stratigraphic events in north Wales, northwest England, southwest Scotland and eastern Ireland, as are those for the *Ulmus* decline. It is likely that local pedological and edaphic factors on the island account for the differences in the first Holocene millennium, while regional climatic factors governed the timings for the rest of the expansions of tree taxa across the wider region, including the Isle of Man. Disturbance, including by human agency, was important at the site scale and perhaps triggered early tree expansion in some places, including Quercus, Ulmus and Alnus. Insularity seems not to have been a significant factor in the expansion of the major forest trees.

Keywords: Isle of Man; Holocene; palynology; trees; climate; isolation; human activity

1. Introduction

Production of pollen profiles for an individual site, the correlation of pollen profiles from several sites within a region and the construction of pollen isochrone maps based on the pollen stratigraphic changes, are all techniques that have been used to investigate the pattern and timing of tree spreading across Europe during the earlier Holocene [1,2]. Maps based on ages for pollen zone boundaries [3,4], particularly the first arrival (the empirical limit) or the point at which a pollen curve rises to sustained higher values (the rational limit), have proven invaluable in understanding the progressive reforestation of the landscape after glaciation, as tree populations responded to climate amelioration [5–11]



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). and expanded from refugia [12–14] to which they had withdrawn during the glacial period. From the context of Britain and Ireland, these refugia were mostly in southern Europe and distant [4], but it is possible that small refugia existed in southern England [15,16] and so of immediate relevance to the Irish Sea area and therefore to the subject of this paper, the Isle of Man. Such isochrone maps have been produced for Ireland [17], for Britain and Ireland as a whole [18,19] and also, for example, for Finland [20], and for Western Europe [1], as well as for North America [21]. However, such tools for reconstructing vegetation changes are only as good as the data upon which they are based, and the existence of many well-dated pollen profiles from which to model spatial changes in tree populations is a fundamental requirement. Most such reconstructions have been at large geographical scales, but it is very likely that there will have been some local scale variability which is not reflected in the spatially coarse studies of large geographical areas. While postglacial climate change is likely to have been the governing background factor in the often rapid rate of tree migration [22–24] and the re-establishment of tree cover across most of Europe [7,10,25,26], in many cases other environmental factors might well have had important influence in addition to climate [27,28]. Altitude, latitude, geology and insularity, for example, are among the factors that could produce a different tree migration history from the more general, broader scale narrative.

In this paper we test the potential for local variability in the timing of early Holocene tree migration and spread by investigating the pollen record of the Isle of Man, a large island (221 square km in area) which has an extensive and well-dated palynological resource within a well-understood broader history of landscape development [29–31]. Our research forms a study in island biogeography and assesses the degree to which local factors were as influential as climate in affecting tree immigration and spread in this spatially concise, localised and insular geographical context. It tests the viability of pollen isochrone maps at any but the largest spatial scales, given the potential variability in the ages of tree establishment at local scales dependent on a range of environmental factors.

2. Environmental Background

The Isle of Man is unique, in the wider context of Britain and Ireland, occupying a position in the centre of the Irish Sea midway between the two much larger landmasses (Figure 1). Holocene pollen records have only recently become available for the Isle of Man [31], but Lateglacial to early Holocene palaeoecological data and the present and historical flora suggest that the island differs floristically from regions surrounding the northern Irish Sea basin. Godwin [32] proposed that the early isolation, small size and limited elevation of the Isle of Man had led to a greatly impoverished flora in comparison with Ireland, Britain and mainland Europe. Birks and Deacon [33] confirmed the status of the Isle of Man as a floristic special case through numerical analyses on the contemporary flora identifying that the island was significantly dissimilar to other regions. It is possible that the relatively small size of the island and its reduced range of available plant habitats and soil types might have been at least partly to blame for the disparity with Britain and Ireland [34], as the Lateglacial and earliest Holocene palaeobotanical record shows that many of the island's native flora were present before severance from Britain [35]. Despite recent introductions the restricted Manx (Isle of Man) flora continues to be impoverished [34,36]. The prehistoric floral and faunal evidence for the Isle of Man [29,37] suggests that the island has formed a distinctive biogeographical unit since deglaciation.

Much of the environmental and biotic diversity of the Isle of Man results from its geomorphology and soils, with the northern plain of the island exhibiting a particularly complex suite of deglacial landforms (Figure 2). This former proglacial plain includes sandur, moraine ridges, alluvial fans and proglacial lake basins. These landforms have created a mosaic of landscape units over a relatively small area [30,31,38,39].



Figure 1. Location of the Isle of Man in the Irish Sea between Britain and Ireland and the location of the following sites mentioned in the text: 1. Port Cranstal 2. Lough Cranstal 3. Curragh y Cowle 4. Ballaclucas (LT5) 5. Ballachrink (LT12) 6. The Cronk 7. Pollies 8. Ballaugh Curragh 6 9. Ballaugh Curragh 21. 10. Quarry Bends 11. Lezayre Curragh 12. Ramsey Harbour 13. Montpellier Bog 14. Beinn y Phott 15. Port y Candas 16. Greeba Curragh 17. Dhoo Valley. There are no pollen sites in the south of the island.

These units, and the soils developed upon them [40], created a wide diversity of edaphic conditions that would have developed over time and influenced the ability of the different tree taxa to colonise and spread, with both organic wetland, clay and fine-grained, well drained soils represented. The Manx uplands, now under shallow peat that began accumulating under a wet climate from ca. 3000 ¹⁴C BP [40–43], form another distinct landscape unit, larger but less diverse, with local tills that reflect the island's time under the ice sheet of the glacial maximum [44,45]) and features such as involutions recording periglacial conditions upon deglaciation [46]. The homogeneity of the upland is broken by the Central Valley of the island, between Peel and Douglas (Figure 1) where alluvium and lowland peat now predominate.



Figure 2. Glacial geomorphology of the northern part of the Isle of Man, after Chadwick et al. [47], also showing the main areas of lowland peat near Ballaugh and in the Lhen Trench.

The existence and tenure of land bridges connecting Britain with the Isle of Man is an important issue that must be considered when discussing the immigration of plant species. Water depths in the northern Irish Sea are deep, particularly to the west of the Isle of Man. Even given maximum isostatic depression and relative sea-level rise, there would still have been deep water between the Isle of Man and Ireland [48]. To the north between the island and Scotland the sea is still relatively deep, but to the east the shelf between England (Cumbria) and the Isle of Man today does not exceed 40 metres in depth and so during periods of relatively low early Holocene relative sea level [49], particularly before 9000 ¹⁴C BP, the Isle of Man will have been connected to Cumbria. The existence and duration of any land bridges is an important factor controlling the palaeoecology of the island, providing a route-way for plants and animals to migrate onto the Isle of Man.

Until the results of a recent research project designed to investigate the history of the Isle of Man's environment became available [31] there was very little information on which to base an interpretation of Holocene vegetation history. Early palynological work was focused on Lateglacial environmental changes, to a large degree because of the recovery of skeletal remains of Giant Deer (Megaloceros) in the tripartite clay/limnic mud/clay successions at the base of the many kettle holes and pingos of the glaciated northern plain of the island (Figure 2), and interest in the environmental habitat of that species. Erdtman [50], Mitchell [51] and Dickson et al. [52] all published pollen data from Lateglacial sediments in these northern depressions but after Erdtman's limited investigation [53] little attention was paid to the overlying Holocene organic sequence. Later work provided Holocene pollen data [54–56], often associated with sea-level studies. More recently, considerable research providing pollen data for reconstructing Isle of Man vegetation history has been undertaken [48,57–60]. While radiocarbon dating of macrofossil wood remains preserved in sediments would be the surest way of dating the presence of particular tree taxa on the Isle of Man, for example the dated Quercus stump from an intertidal peat bed at Port Cranstal [61] which produced an age of 7970 ± 30 BP [8826 cal. BP]. This timing agrees well with dates based on the pollen data, see below, but sub-fossil wood remains identified

to taxon level are very rare on the island, and seldom dated. Reconstruction of the native arboreal history of the Isle of Man must therefore be based upon the available pollen data.

This paper has three main aims, first to summarise early Holocene data from seventeen sites from across the Isle of Man, second to identify the evidence for and the timing of the rational limits of the main tree taxa, and third to evaluate the sequence of early Holocene succession on the Isle of Man in comparison to the surrounding regions, assessing the relative roles of the main environmental factors in effecting changes in forest establishment and evolution.

3. Materials and Methods

3.1. Methodology

For this study, seventeen pollen sites have been included (Figure 1), selected on the basis of preservation of early to mid-Holocene stratigraphy and radiocarbon dating of rational limits, as well as the *Ulmus* decline which defines the end of the mid-Holocene period. Pollen diagrams were produced for the entire profile at each site, but only the earlier Holocene time periods are presented here, approximately 11,700–5800 cal. BP, and only the tree pollen curves, the subject of this paper. Pollen analyses were undertaken following standard techniques, with preparation following Moore et al. [62], including HF for minerogenic samples. Identifications were made with reference to Moore et al. [62], Faegri and Iversen [63] and type collections. Pollen nomenclature follows Stace [64] and Bennett et al. [65]. At all the sites pollen sums are based upon total dryland pollen excluding all aquatics and spores but including *Alnus*. Percentage pollen diagrams were constructed using TILIA and TILIAGRAPH [66,67].

3.2. Radiocarbon Dating

Thirty-one radiocarbon measurements are available to provide chronologies for the sites, although some of them provide only limiting ages. All radiocarbon ages were calibrated using OxCal4.4 and IntCal20 [68] and are listed on Table 1 giving the 2σ confidence interval in calibrated years BP as well as the mid-range calibrated age BP. Radiocarbon ages are cited in the text with the mid-range calibrated age in brackets. Almost all dates were obtained by the AMS technique on small bulk samples of peat, although one date is radiometric on a larger sample and is identified on Table 1.

Table 1. Radiocarbon ages, including limiting dates, for major Isle of Man early and mid-Holocene tree pollen stratigraphic events. Dates are AMS on peat, except Dhoo Valley 16 (radiometric). Age ranges (2δ) and the mid-range age are derived from calibration results using Oxcal 4.4 and IntCal20 [68].

Pollen Feature	¹⁴ C Date BP	Lab. Code	28 Age Range (cal. BP)	Mid-Range Age (cal. BP)	Site
Ulmus decline	4785 ± 55	AA-39112	5320-5600	5460	Montpellier Bog
	$>4980 \pm 50$	AA-34512	5590-5900	5745	Port-y-Candas
	5200 ± 35	Poz-88363	5900-6170	6035	Ballachrink LT12
	5310 ± 70	AA-28379	5930-6280	6105	The Cronk
	5313 ± 38	UB-3555	5940-6270	6105	Dhoo Valley 16
Pinus rise	$<6860\pm55$	AA-28383	7580-7830	7705	Port Cranstal
	7020 ± 35	SUERC-2603	7750-7940	7845	Quarry Bends
	7045 ± 35	SUERC-2604	7790-7960	7875	Pollies
	7470 ± 35	SUERC-2620	8200-8370	8285	Montpellier Bog
Main Alnus rise	6680 ± 55	AA-45405	7430-7670	7550	Montpellier Bog
	$>6730 \pm 100$	AA-29738	7420-7780	7600	Ballaclucas LT5
	6865 ± 45	AA-52529	7600-7830	7715	Lezayre Curragh
	$<6860\pm55$	AA-28383	7580-7830	7705	Port Cranstal
	7045 ± 35	SUERC-2604	7790-7960	7875	Pollies
	7105 ± 80	AA-29740	7730-8170	7950	Ballachrink LT12
	7370 ± 35	SUERC-2602	8030-8320	8175	Quarry Bends

Pollen Feature	¹⁴ C Date BP	Lab. Code	28 Age Range (cal. BP)	Mid-Range Age (cal. BP)	Site
Main Ulmus and	7540 ± 75	AA-29741	8180-8520	8350	Ballachrink LT12
Quercus rises *	8115 ± 65	AA-45404	8770-9290	9030	Montpellier Bog
	8220 ± 35	SUERC-2605	9020-9400	9210	Pollies
	8265 ± 40	SUERC-2600	9030-9420	9225	Curragh y Cowle
	8290 ± 35	AA-29335	9130-9430	9280	Ballaugh Curragh 21
	$< 8770 \pm 50$	AA-52525	9550-10120	9835	Ramsey Harbour
Main <i>Corylus</i> rise	8160 ± 75	AA-29742	8780-9410	9095	Ballachrink LT12
·	8870 ± 85	AA-29737	9670-10,230	9950	Curragh y Cowle
	9030 ± 40	SUERC-2611	9960-10,250	10,105	Ballaugh Curragh 21
	9110 ± 35	SUERC-2606	10,190-10,380	10,285	Pollies
	$<9150\pm70$	AA-36488	10,200-10,500	10,350	Montpellier Bog
	$> 9390 \pm 40$	SUERC-2615	10,500-10,720	10,610	Ramsey Harbour
Main <i>Betula</i> rise	9275 ± 50	AA-48013	10,260-10,580	10,420	Curragh y Cowle
	9320 ± 55	AA-48012	10,300-10,690	10,495	Pollies
<i>Juniperus</i> peak	9450 ± 100	AA-32034	10,420-11,150	10,785	Pollies
Juniperus rise	9745 ± 40	SUERC-2614	10,900–11,250	11,075	Ballaugh Curragh 6

Table 1. Cont.

* Ages refer to both rises except for Montpellier Bog which refers to Quercus only.

3.3. Tree Immigration Maps

Radiocarbon ages for the earlier Holocene rational limits of the major tree taxa from the Isle of Man and from adjacent areas around the northern Irish Sea are shown on a series of distribution maps. Letter codes for the Isle of Man sites are shown. References and date calibration ranges for the adjacent area sites are shown in Supplementary File S1. More ages are available for some pollen stratigraphic boundaries than others, for example the *Ulmus* decline has received considerable dating attention whereas the *Quercus* and *Ulmus* rational limits much less so. While probably not comprehensive, enough ages are available to allow comparison between the island and adjacent areas.

4. Palaeoecological Sites and Data

Arising from research associated with the New History of the Isle Man: Volume 1 'Evolution of the natural landscape' book [31] there are now many radiocarbon-dated pollen diagrams from which we can reconstruct the early to mid-Holocene vegetation history of the Isle of Man (Figure 1). These sites include the northern plain at Cranstal, Curragh y Cowle, the Lhen Trench, The Cronk, Pollies, Ballaugh Curragh, Lezayre Curragh and Ramsey Harbour, in the uplands from Montpellier Bog and Beinn y Phott, and in the central valley peatlands at Port y Candas, Greeba Curragh and the Dhoo Valley. Research on the vegetation history of the Manx Uplands has lagged behind other upland areas within Britain and Ireland, with the lack of palaeoecological data stemming from the paucity of appropriate sites, organic peat soils being generally shallow and of late Holocene age [43]. The Montpellier and Beinn y Phott sites can be assumed to be representative of the uplands, which is a fairly homogeneous landscape unit. Individually none of these sites spans the entire Holocene, but there is considerable chronological overlap between sites and correlation of the pollen data allows reconstruction of vegetation changes. Each site has an abbreviation letter code, shown in parenthesis in the following descriptions, which is used to identify it on the radiocarbon maps for each taxon.

4.1. Cranstal (C)

Lough Cranstal (NX 455025) is a low-lying lagoonal basin on the northern margin of the Bride Moraine (Figure 1, site 2). The lagoon consists of two basins at an altitude of nine metres and is bounded to the north by a low ridge of till. Lough Cranstal is currently an alder carr/minerotrophic fen and *Phragmites, Menyanthes, Alnus* and *Equisetum* are the dominant plant species. The lower sediments are limnic, overlie the basal till and

comprise silts, sands and clays formed by erosion of the surrounding till ridges during the early Holocene. These more inorganic deposits are overlain by limnic and detrital peats that accumulated in a shallow lake to fen environment from around 7370 ± 110 BP [8182 cal. BP]. Palaeoecological data (pollen and diatoms) are available for the basin [54] including the mid-Holocene *Ulmus* decline, although this remains undated here. A rise in *Alnus* percentages occurs around the level of the radiocarbon age at 7370 ± 110 BP but as it coincides with a major lithological change from clay to organic sediments it might not be reliable, even though it agrees well with the age from nearby Quarry Bends (see below). As well as providing a mid-Holocene pollen record Lough Cranstal is important for the reconstruction of early Holocene sea-level history. Nearby Port Cranstal (NX 247501; Figure 1, site 1) contains mid-Holocene estuarine and lagoonal sediments in coastal exposures which include peat deposits with tree remains [56,61]. An age on the top of the peat of 6860 \pm 55 BP [7705 cal. BP] with very low *Alnus* frequencies (Figure 3) provides a limiting age for the *Alnus* pollen rise.





4.2. Curragh y Cowle (CC)

Curragh y Cowle (NX 411020) is a kettle-hole basin on the southern flanks of the Bride/Jurby Hills in the northern plain of the Isle of Man (Figure 1, site 3) which comprises an undulating terrain of glacigenic tills, moraine ridges, proglacial outwash sandar and lacustrine sediments, with large alluvial sand and gravel fans issuing from the Manx uplands to the south. There are many such depressions within the sandur plain terrain. At the base of these deep depressions typical tripartite Lateglacial sediment sequences occur, with a succession of clastic/organic/clastic units representing deposition under stadial, interstadial and renewed stadial conditions. Recent research at Curragh y Cowle has produced a full early Holocene vegetation history, the arboreal components of which are shown in Figure 3. The pollen data contains evidence for the rational limits of *Betula*, *Corylus*, *Ulmus* and *Quercus*, all of which have been radiocarbon dated.

4.3. The Lhen Trench (LT5 and LT12)

The Lhen Trench forms a broad curve from the north coast north-east of Ballaugh Curragh. It is a 4 km long, 200 m wide valley, now containing the small Killane River, which is incised into glacial deposits in the northern plain of the island (Figures 1 and 2). It has been attributed to incision by a glacial outwash system issuing from the Irish Sea ice sheet ca. 21,000 cal. BP [69–71], draining into the glacial lake at the foot of the Manx upland where the Curraghs are today. After ice retreat, the Lhen Trench sustained little fluvial activity and throughout the Holocene it has been a low-lying wetland, accumulating 3–4 m of peat in the centre, where peat inception occurred around 9000 cal. BP. Ballaclucas LT5 (NX 378009;

Figure 1, site 4) contains lithostratigraphic evidence of fluctuations in mid-Holocene sea level [48] and a limiting radiocarbon age for the *Alnus* pollen rise (Figure 4). Ballachrink LT12 (NX 394002; Figure 1, site 5) contains pollen evidence for the rational limits of *Corylus*, *Ulmus*, *Quercus* and *Alnus* (Figure 4). The radiocarbon ages for the increases in *Alnus*, *Quercus* and *Ulmus* pollen are acceptable, whereas the age for the *Corylus* rise appears to be very young and might be in error. It does, however, constrain the completed *Corylus* rise, the start of which might well be some centuries earlier, given the amorphous and slowly accumulating peat at this site.



Figure 4. Percentage pollen diagrams from Ballaclucas LT5 and Ballachrink LT12, Isle of Man, showing selected tree taxa and ¹⁴C BP AMS ages.

4.4. The Cronk (TC)

The Cronk (SC 336963) is a complex sequence of Late Devensian glaciolacustrine and fluvioglacial sediments overlain and truncated by a wide channel exposed in coastal cliff section on the west coast (Figure 1, site 6). The channel is filled with peat, grading upwards into river gravel and back-channel deposits. The base of the peat contains high *Alnus* and *Ulmus* pollen frequencies and so is of mid-Holocene age. The upper part of the peat is dated to the early Bronze Age. Fluvial gravels overlying the peat contain fragments of charcoal and thermally fractured stones, materials that are typical of a prehistoric 'burnt mound'. The mid-Holocene peat bed and organic soil sequence is exposed in section. All of the tree pollen taxa had reached their rational limits before The Cronk peat began accumulating, but the pollen data (Figure 5) reveals a well-defined *Ulmus* decline low in the profile that has been dated to 5310 \pm 70 BP [6105 cal. BP].

4.5. Pollies (PO)

Pollies (SC 348946) is a large basin on the surface of the alluvial fan issuing from Glen Dhoo west of Ballaugh Curragh (Figure 1, site 7). In addition to the many kettle holes that occur within the deglaciated terrain of the Isle of Man, there are also likely pingo remnant features on the alluvial fans at the foot of the upland, particularly on the large fan near Ballaugh. Again, tripartite Late Glacial sediment sequences occur at the base of these depressions below variable thicknesses of Holocene lacustrine muds and peats. Most of the interstadial sediments are lake marls and it is in these units that most of the Giant Deer remains have been found. Pollies is only a few hundred metres from the depression at Loughan Ruy, which contained radiocarbon dated *Megaloceros* remains [56]. A new AMS-dated early Holocene pollen sequence has been produced from the overlying organic deposits at Pollies and provides important information on the early Holocene vegetation history. Pollies contains a comprehensive picture of the pollen stratigraphic changes during the earlier Holocene (Figure 5), with increases to the rational limits of *Juniperus*, *Betula*, *Corylus*, *Ulmus* and *Quercus*, as well as the *Alnus* empirical rise, all of which have been radiocarbon dated.



Figure 5. Percentage pollen diagrams from The Cronk and Pollies, Isle of Man, showing selected tree taxa and ¹⁴C BP AMS ages.

4.6. Ballaugh Curragh and Quarry Bends (BC6, BC21 and QB)

Ballaugh Curragh is the most extensive wetland on the Isle of Man (Figure 1, sites 8–10) nestling between two large mountain front alluvial fans at Sulby and Ballaugh (Figure 2). Peat deposits accumulated over a formerly extensive proglacial lake that existed while the Devensian ice margin was near Jurby. This former lake basin provided a flat terrain ideal for the development of a substantial wetland, with impeded drainage producing blue-grey lacustrine clays and encouraging subsequent peat inception during the early Holocene [72]. Systematic investigation of the peat stratigraphy produced transects of cores across the bog traversing west-east across the northern part and north-south across the western part of the peat basin. There is little variation in surface altitude and the bog appears to have a virtually flat surface. The Holocene stratigraphy contains four major units with blue-grey silty clays overlain and intercalated with organic limnic gyttja comprising the basal units which overlie a thick succession of proglacial laminated late Devensian lake sediments. Mid-profile, detrital peats and gyttja (organic lake muds) form a thick (2 metre) sequence, which in turn is overlain by an uppermost 1 metre unit of fresh turfa peat. The fresh surface turfa peat reflects a hiatus or truncation within the stratigraphy, with regrowth after cutting although an original turfa peat probably survives in places. Pollen analysis has been carried out (Figure 6) on peat profiles at cores BC6 (SC 357952) and BC21 (SC 368953) where peat deposits were deepest in the northern part of the wetland. A site at Quarry Bends (SC 368942), at the southern limit of the Ballaugh Curragh wetland, was also analysed (Figure 7), and all three profiles have been radiocarbon dated. Wetland sedimentation has taken place at Ballaugh Curragh throughout the Holocene and the sediments are an invaluable archive of Holocene vegetation history. BC6 contains sediments that formed during the earliest Holocene and provides data for the empirical limit of *Juniperus* and its subsequent rise to high frequencies. Core BC21 contains a more comprehensive picture of the vegetation changes throughout the earlier Holocene, including the increases to rational limits of Corylus, Ulmus, Quercus and Alnus, with the first three radiocarbon dated. Although not dated at BC21, the *Alnus* rise is dated at Quarry Bends to 7370 \pm 35 BP [8175 cal. BP].



Figure 6. Percentage pollen diagrams from Ballaugh Curragh 6 and Ballaugh Curragh 21, Isle of Man, showing selected tree taxa and ¹⁴C BP AMS ages.





4.7. Lezayre Curragh (LC)

Lezayre Curragh is a formerly extensive wetland located between two large mountain front alluvial fans at Sulby and Glen Auldyn (Figure 1, site 11). The curragh existed as a large alluvial swamp and the surface of the basin is marked by anastomising palaeochannels. The sedimentology is very variable, and coring reveals a mixed sequence of alluvial floodplain, flood-gravel and organic deposits. The Holocene succession overlies a formerly extensive proglacial lake that was impounded against the Manx upland between Ramsey and Ballaugh Curragh (Figure 2). This former glacial lake basin provided a flat terrain ideal for slowing the flow of the Sulby River which emptied into this swamp. Systematic investigation of the stratigraphy has identified former channel fills, buried basal peat deposits and substantial quantities of buried wood preserved in the peat. Radiocarbon dated pollen data is available for the basal peat deposits, which reveals an early Holocene sequence of vegetation changes. Mid-Holocene pollen is available from various channel fills within the basin. Historical records and the stratigraphy suggest that Lezayre Curragh remained an impenetrable woodland swamp through the Holocene until modern drainage. Pollen from compressed basal peat deposits (Figure 7) contains the rational limits of Quercus, Ulmus and *Alnus* which unusually occur at the same time. The radiocarbon age for these features is 6865 ± 45 BP [7715 cal. BP], which is as expected for *Alnus*, but very late for the others. The age has been accepted for *Alnus* in this paper, but the others have not been used at present.

4.8. Ramsey Harbour (RH)

The site at Ramsey Harbour (SC 454947) is a thin intertidal peat exposed on the foreshore (Figure 1, site 12) and formed from detrital organic sediment that contains a lot of *Betula* wood. It overlies glacial clay sediment. Pollen analysis shows that it formed during the early Holocene and has been overtaken by the mid-Holocene sea-level maximum. No intertidal sediments have been preserved, although the peat provides a limiting age for sea-level rise. The *Corylus* rise occurs within the pollen record (Figure 8) and has been dated to after 9390 \pm 40 BP [10,610 cal. BP].

Ramsey Harbour

Montpellier Bog



Figure 8. Percentage pollen diagrams from Ramsay Harbour and Montpellier Bog, Isle of Man, showing selected tree taxa and ¹⁴C BP AMS ages.

4.9. Montpellier Bog (MB)

Montpellier Bog (SC 362883) is small-scale valley mire within Druidale in the valley of the river Sulby in the northern uplands of the island where ca. 2–3 metres of peat have accumulated (Figure 1, site 13). Geomorphological interpretation of the development of Druidale [73] suggests that during the late Devensian the river followed a path across the mire, whilst an adjacent gorge was filled with glacial and solifluction sediments. Fluvial erosion excavated the gorge during the late Devensian capturing the river and leaving the current mire as a large flat expanse of former floodplain. Subsequently 2–3 metres of peat have accumulated forming the current mire. Chronology for the pollen analysis (Figure 8) is provided by four radiocarbon ages which demonstrate that peat accumulation began during the early Holocene at 9150 \pm 70 BP [10,350 cal. BP]. Montpellier Bog contains a comprehensive picture of the vegetation changes in the Manx Uplands during the early Holocene, with the increases to rational limits of *Pinus*, *Quercus* and *Alnus*, all of which have been radiocarbon dated (Table 1). *Betula* and *Corylus* were present at the base of the profile and ages are limiting for those curves. An *Ulmus* decline dated 4785 \pm 55 BP [5460 cal. BP] occurs higher in the profile.

4.10. Beinn y Phott

Beinn y Phott (SC 386867) provides a radiocarbon dated blanket peat profile from the northern uplands of the Isle of Man (Figure 1, site 14) that begins in the mid-Holocene at 6240 ± 60 BP [7126 cal. BP]. The lower peat is very well humified and an undated *Ulmus* decline occurs a few centimetres above the base of the profile. The rest of the peat is Late Holocene in age [59]. Older blanket peat is rare in the uplands of the Isle of Man because of peat cutting [43] and this site has allowed the reconstruction of climate before and around

the *Ulmus* decline through peat humification studies and bog surface wetness [59,74]. This profile does not provide a direct age for a tree pollen boundary and so the pollen diagram has not been reproduced in this paper.

4.11. Port-y-Candas (PC)

Port-y-Candas (SC 285816) is a small area of curragh wetland in the Central Valley east of Peel (Figure 1, site 15) that has considerable archaeological significance [59]. The early Medieval archaeological site of Port-y-Candas consists of an almost circular platform surrounded by a pair of banks and ditches. The site is located on the edge of a wetland basin. Recent stratigraphic and pollen analytical work [59,75] from peat deposits located within the wetland basin (Figure 9), recorded vegetation history beginning in mid-Holocene times. Radiocarbon dating has shown that peat inception at site PYC60 occurred at 6140 \pm 70 BP [7047 cal. BP]. The *Ulmus* decline is faint at PYC60 but is recognised in mid-profile immediately below a radiocarbon age of 4980 \pm 50 BP [5745 cal. BP].



Dhoo Valley 16



Figure 9. Percentage pollen diagrams from Port y Candas 60 and Dhoo Valley 16, Isle of Man, showing selected tree taxa and ¹⁴C BP AMS ages.

4.12. Greeba Curragh

Greeba Curragh (SC 314804) is an extensive area of curragh wetland in the island's central valley (Figure 1, site 16). Peat depths of around 3 metres occur towards the centre of the valley, within 20 m of the river Neb and these were sampled for pollen analysis. The peat is largely fibrous, consisting of sedge and grass remains but with wood fragments. A radiocarbon age of 5940 ± 80 BP [6770 cal. BP] at the base suggests that less than 7000 calendar years of palaeoecological record should be available at this site. Four radiocarbon ages secure the sequence [76]. An *Ulmus* decline occurs low in the profile but is undated. All the main tree taxa had reached rational limits by the time peat began accumulating at Greeba Curragh, however the increase in *Fraxinus* is well represented and occurred at an interpolated age of ca. 5800 cal. BP, at the same time as the *Ulmus* decline, a characteristic age for that feature. As this profile does not provide a direct age for a tree pollen boundary the pollen diagram is not reproduced in this paper.

4.13. Dhoo Valley (DV)

The valley of the river Dhoo, which occupies the eastern part of the island's Central Valley, contains substantial peat deposits, in many places concealed by recent alluvium. Although mainly shallow and of recent formation, in places the peat began to accumulate in the mid-Holocene [55]. The pollen frequencies from the base of the peat at Dhoo Valley 16 (SC 339777; Figure 1 site 17) contain a decline in *Ulmus* pollen values (Figure 9) which is dated to 5313 ± 38 BP [6105 cal. BP] and represents the mid-Holocene *Ulmus* decline.

5. Discussion

5.1. Early to Mid-Holocene Tree Spreading in the Isle of Man

The Isle of Man radiocarbon measurements for major Holocene pollen-stratigraphic boundaries are listed in Table 1, which shows the ¹⁴C ages, their calibrated age range BP and their mid-range age (cal. BP). The listed sites are located in Figure 1. These measured ages are followed in brackets by their mean calibrated ages in the following discussion and are compared with the radiocarbon ages for the same boundaries from British and Irish sites around the northern Irish Sea which are listed and calibrated in Supplementary File S1. It should be pointed out that most Isle of Man ages come from sites on the island's geologically distinct lowland northern plain (Figure 2) which at present must be assumed to be representative of the vegetation history of the whole island.

5.1.1. Pre-Woodland Succession and the Juniperus Maximum

Radiocarbon dated pollen data from Pollies and Curragh y Cowle suggest that prewoodland grass and low shrub communities persisted as the dominant vegetation type on the northern coastal plain for a long period of time in the early Holocene. Succession towards woodland started with the increase in *Juniperus* which took place at Ballaugh Curragh 6 at 9745 \pm 40 BP [11,075 cal. BP], the only dating available for this pollen stratigraphic feature on the island. Rising Juniperus frequencies culminated in a peak which is a clear transitional pollen marker between earlier rich grass-heath and established Betula open woodland and is likely to have occurred at different times in western Britain [77], although the Juniperus peak consistently occurs significantly before the Betula rational limit on the region's pollen diagrams [78,79]. The major peak in Isle of Man Juniperus percentages has been radiocarbon dated at Pollies to 9450 ± 100 BP [10,785 cal. BP]. On Lateglacial fluvioglacial coversand soils at Knowsley Park in southwest Lancashire [80] a similar high peak of Juniperus, followed by a period of Betula and Salix dominance, culminated at 9305 ± 65 BP [11,075 cal. BP], very similar to the Isle of Man age. In the regions adjacent to the northern Irish Sea the peak of Juniperus is significantly earlier (Figure 10), ranging from 9600 to before 10,000 radiocarbon years ago as succession to *Betula* woodland took place more swiftly than on the island. Its regional variation might reflect local environmental factors.

5.1.2. The Betula Rise

The information for the northern Irish Sea region and the direct comparison with dates on the spread of *Betula* in adjacent areas of Britain and Ireland (Figure 11) shows the Manx ages to be significantly later. The *Betula* rise at several sites in Northern Ireland [3], at Scaleby Moss in Cumbria [81], at Bigholm Burn in southwest Scotland [82] and at Red Moss in Lancashire [83] occurs around 12,900–12,200 cal. BP. Innes et al. [58] have discussed the delayed expansion of *Betula* pollen on the Isle of Man, where the *Betula* rise to its rational limit is dated to around 10,400 cal. BP, with radiocarbon ages of 9275 \pm 50 BP [10,420 cal. BP] at Curragh y Cowle and 9320 ± 55 BP [10,495 cal. BP] at Pollies [84]. The establishment of closed birch woodland on the northern plain of the island seems to have occurred about 600 years later than in other areas around the northern Irish Sea basin where it is recorded at around 9800 radiocarbon years ago or earlier, although some sites in Northern Ireland have ages closer to the Isle of Man figure (Figure 11). Data from the Ramsey Harbour peat deposit reveal that Betula was present in low numbers shortly after 9450 ± 70 BP [10,792 cal. BP] and in the Manx Uplands the basal deposits at Montpellier Bog (Figure 8) demonstrate that *Betula* had spread before 9150 ± 70 BP [10,350 cal. BP], both agreeing well with the dated horizons at Pollies and Curragh y Cowle. Although probably present regionally at an earlier stage in favoured locations, environmental constraints of climate and soils may have delayed *Betula* expansion [2,85,86]. It appears that for several centuries, perhaps much of the first Holocene millennium, parts of the northern plain of the Isle of Man supported rich grassland and latterly low shrub vegetation rather than woodland. This persistence of pre-forest environments meant that the expansion of Betula



woodland occurred much later in this part of the Isle of Man than in adjacent areas of Britain and Ireland.

Figure 10. Radiocarbon ages for the *Juniperus* maximum in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.

5.1.3. The Corylus Rise

The eventual establishment of closed woodland conditions, likely to be a diachronous event between the outwash and till areas of the northern plain and the upland, caused the shading out and suppression of the early Holocene open herb-heath-shrub communities by continuous tree cover. Birch and willow woods were ubiquitous in the lowlands, with the latter probably more favoured in wetter areas. The *Corylus* rise is dated at Curragh y Cowle, Pollies and Ballaugh Curragh 21. A typical age is 9030 \pm 40 BP [10,105 cal. BP] at Ballaugh Curragh 21 when pollen data identifies the rise to co-dominance of *Corylus* at the site. The very late *Corylus* rise age at Ballachrink LT12 can be discounted for reasons explained above, being later than the rational limit. At Ramsey Harbour the *Corylus* rise occurs midway between radiocarbon dated horizons of 9450 \pm 70 BP [10,792 cal. BP] and 8770 \pm 50 BP [9835 cal. BP]. *Corylus* pollen is present in substantial quantities at the base of the Montpellier Bog profile dated to 9150 \pm 70 BP [10,352 cal. BP], which provides a limiting age as the rational limit must be older than that. The addition of hazel to the woodlands of



the Isle of Man increased the density of the canopy and finally shaded out any surviving lowland juniper. *Salix* also would have declined although surviving in wetland situations.

Figure 11. Radiocarbon ages for the *Betula* rise in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.

Corylus therefore became established in both the northern lowlands and uplands of the Isle of Man around or before 10,200–9600 cal. BP but again, as with almost all of the main vegetation changes, was probably diachronous across the area depending upon local edaphic and other environmental factors. The radiocarbon age from Curragh y Cowle of 8870 \pm 85 BP [9950 cal. BP] is the latest acceptable age on the island but is similar to several late ages in Britain and Ireland (Figure 12), the range of variation probably caused by local edaphic factors. Hazel propagates through the dispersal of nuts, which are transported by a variety of mechanisms including by animals (birds, rodents, etc.), deliberate or accidental spreading by humans and by water [2]. There has been considerable debate amongst palaeoecologists over the role people have played in the early Holocene expansion of hazel [87–91] through the use of fire (see below) but any link between people's activities and the hazel rise must be circumstantial, as is also the case for Britain and Ireland. Comparisons with *Corylus* rise ages in the northern Irish Sea region (Figure 12) show that there is no difference in the timing or the range of ages for this pollen boundary between



centuries around 9000 14 C BP, as expected from the national data of Britain and Ireland as a whole [2,3].

Figure 12. Radiocarbon ages for the *Corylus* rise in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.

5.1.4. The Ulmus and Quercus Rises

The thermophilous deciduous trees *Quercus* and *Ulmus* were the next major components of the Holocene forest to rise to prominence and their rational limits can be considered together as they usually occur within the same chronological range. In most pollen diagrams *Quercus* is easily the more abundant of the two, but in the Lhen Trench at Ballachrink (LT12) *Ulmus* is present in consistently higher frequencies. Here, the immigration of oak and elm occurs together at 7540 \pm 75 BP [8350 cal. BP]. At Lezayre Curragh the *Quercus* and *Ulmus* increases are radiocarbon dated to 6865 \pm 45 BP [7715 cal. BP], an exceptionally late age which might well be erroneous. Further dated lowland examples of the increase to rational limits of *Quercus* and *Ulmus* are present at Ballaugh Curragh 21, Pollies and Curragh y Cowle, all with radiocarbon ages close to 8200 ¹⁴C BP (ca. 9200 cal. BP). In the Manx Uplands at Montpellier Bog *Quercus* and *Ulmus* reach their rationale limits shortly before a radiocarbon age of 8115 \pm 65 BP [9030 cal. BP], very similar to the lowland examples. Although chronologically similar, significant variation occurs at this time in the frequencies of these major forest trees from site to site and it appears that their importance in forest composition showed considerable spatial differences.

Comparison of the range of radiocarbon ages for the *Ulmus* and *Quercus* rises with the Isle of Man sites (Figures 13 and 14) shows that there is no significant difference between those on the island and those in Britain and Ireland, the mean ages and the range of the ages being the same. While the ranges are wide, with some dates very early, as at Roddan's Port in Northern Ireland [92] (S26 and S23 on Figures 13 and 14) or very late as in some Scottish sites, this variation can be attributed to local factors, perhaps edaphic or altitudinal. There also seems to be no clear latitudinal variation, although it might be expected that expansion of the two trees would be later at more northerly sites, this appears not to be the case except in a few examples, for both taxa.



Figure 13. Radiocarbon ages for the *Ulmus* rise in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.



Figure 14. Radiocarbon ages for the *Quercus* rise in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.

5.1.5. The Pinus Rise

Pinus does not become important in the Isle of Man until after oak and elm have become fully established in the forest. A short-lived period of high pine frequencies is a consistent feature of lowland woodland history at a number of pollen sites on the island between about 7500 and 7000 ¹⁴C BP (Figure 15). Across the northern plain there are major differences in relative percentages at the pine maximum over relatively small distances, with pine reaching 30% of total land pollen at Pollies, less than 10% of total land pollen at Ballaugh Curragh 21, yet briefly attains almost 80% at Quarry Bends (Figure 7). As the pollen percentage of *Pinus* which is accepted as evidence of presence rather than long-distance transport is 5% [93], however, pine was clearly present and common on the island. Pine percentages of 20–30% at Ballachrink (LT12) and Port Cranstal perhaps point to the more average pine representation across the area as a whole. In general, however, a forest mosaic with substantial spatial differences in all tree abundances across the northern plain seems to be demonstrated by the pollen data. In the Manx Uplands the lower values of pine encountered at Beinn-y-Phott are interesting because at Montpellier Bog, only 2 km away, pine is abundant between ca. 7600 and 5400 cal. BP.



Figure 15. Radiocarbon ages for the *Pinus* rise in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.

The proximity of the two sites and the quantity of pine pollen at Montpellier Bog possibly reflects local Scots Pine woodlands around the site. Montpellier Bog records a pine decline dated to after 4785 ± 55 BP [5460 cal. BP], with a further undated decline after ca. 4000 years ago, a similar age to that of a widespread pine decline in north-west Britain and Ireland [94], after which there is a hiatus in the sequence with the uppermost peat from the late Holocene. The existence of local *Pinus* populations persisted at altitude into the Neolithic, at least locally at Montpellier Bog [73], but these had gone by ca. 5400 cal. years BP, perhaps because of the climatic deterioration around that time.

The arrival and expansion of pine is variable in character on the Isle of Man, for example the extremely high frequencies encountered ca. 8500–7500 cal. years ago at Quarry Bends on the edge of Ballaugh Curragh adjacent to the Sulby Glen alluvial fan. The location of Quarry Bends very near to the uplands may account for its very high peak values, as pine frequencies of 30% total land pollen with peaks above 60% occur between ca. 8500–5500 cal. BP at Montpellier in the northern uplands. These data extend the known rational limits of pine [95] in Britain and Ireland and are late for the event compared to the radiocarbon ages in Britain and eastern Ireland (Figure 15), although similar to those in northern Ireland. Pine appears not to have been a significant component of the forests in many parts of

the region. More ages are needed for this pollen zone boundary in the northern Irish Sea region.

5.1.6. The Alnus Rise

The Ballaugh Curragh, Lezayre Curragh and Lhen Trench pollen profiles reveal that Alnus increased sharply during the mid-Holocene after the rational limits of Quercus and Ulmus. Within Ballaugh Curragh at Quarry Bends and BC21 Alnus appears to replace Pinus, perhaps directly on increasingly wet peat surfaces. The spread of Alnus within the woodland is dated 7105 \pm 80 BP [7950 cal. BP] at Ballachrink (LT12) in the Lhen Trench and to 6865 ± 45 BP [7715 cal. BP] at Lezayre Curragh. Increased climatic wetness in the mid-Holocene may well have led to the direct replacement of pine by alder in the lowland wetlands, although at Ballachrink (LT12) moderate pine frequencies are little affected by the increase in alder, Corylus being the main declining curve when alder rises. The Alnus rise is also dated at Montpellier Bog to ca. 6680 ± 55 BP [7550 cal. BP], although it is gradual and difficult to define. Mid-Holocene pollen data from Beinn-y-Phott do not contradict this vegetation history, where the basal peat dated to 6240 ± 60 BP [7126 cal. BP] is suggestive of an upland landscape covered by oak, elm, alder and hazel woodland. Clearly by at least 7610–7485 cal. BP all the main components of the mixed deciduous forest were present in the Manx Uplands, with the only areas not forested probably being the larger expanses of blanket peat (e.g., Beinn-y-Phott), localised clearings and the rocky summits of the Manx hills. After the spread of *Alnus* through the upland and lowland woodlands, the assembly of the mid-Holocene mixed forest was complete on the Isle of Man.

The mid-Holocene rise of *Alnus* pollen is one of the most significant elements of Manx vegetation history, often occurring sharply and at a variable period after its first appearance in the pollen record. In large lowland wetlands such as the Ballaugh Curragh alder rose to abundance, whereas around smaller wetland sites its increase is not so great, perhaps reflecting more diverse woodlands on the surrounding drier soils of moraine ridges and sandur surfaces. As noted by Gieseke and Brewer [24], *Alnus* is usually present well before its eventual expansion, and so it had probably spread to the Isle of Man much earlier, perhaps while the island was still connected to England around the Late Devensian-Holocene transition. *Alnus* certainly rose to prominence ca. 8050–7700 cal. BP on the Isle of Man, an age which is in close agreement with the mean ages for the feature [96] around the Irish Sea province (Figure 16), for example ca. 8000–7800 cal. BP at Red Moss, Lancashire [83], ca. 7700–7200 in southwest Scotland [82] and 7600 cal. BP in northeast Ireland [97]. Despite its insular situation there was no delay in the *Alnus* rise on the Isle of Man, suggesting a climatic trigger for its regional expansion.

5.1.7. Later Tree Arrivals and the Ulmus Decline

A major decline in *Ulmus* pollen frequencies ca. 5800 cal. BP defines the end of the mid-Holocene phase of maximum extension of forest cover in most areas of Britain and Ireland [98]. There are enough examples of this late mid-Holocene *Ulmus* pollen decline in the Isle of Man, although it is absent at some sites because erosion, peat cutting or marl digging has removed the relevant sediments, as at Pollies and Curragh y Cowle, to allow comparison with the age of this major pollen-stratigraphic feature in the areas around the northern Irish Sea. Some Ulmus declines on the Isle of Man are undated, as at Greeba Curragh, and the first securely dated lowland Manx example was from The Cronk (Figure 5), although a faint feature on the pollen diagram. The age of 5310 ± 70 BP [6105 cal. BP] agrees well with many Ulmus-decline ages from lowland Britain and Ireland (Figure 16). It has since been confirmed by Manx ages of 5313 ± 38 [6105 cal. BP] from Dhoo Valley 16 and 5200 ± 35 [6035 cal. BP] from Ballachrink LT12. Indications of smallscale forest opening accompany the Ulmus decline at The Cronk and Ballachrink, which may indicate the role of early farmers in this vegetation change, although the death of elm trees through natural causes may also create the conditions of temporary canopy opening [99,100]. Such natural causes could have included climate deterioration, soil

acidification or the effects of a pathogen [98,101], and the decline in elm pollen frequencies should best be regarded as multi-causal and site specific, with more than a single decline often recorded in a pollen profile [102] and likely to have different causes. In western Ireland, Lamb and Thompson [103] note that elm frequencies recover strongly after the decline, unlike in Britain, and so a pathogen might have been less important there. Little elm recovery occurs in the Isle of Man examples. The absence of elm pollen frequencies at Montpellier Bog above a ¹⁴C age of 4785 ± 55 BP [5460 cal. BP] provides the only evidence from the Manx Uplands for an event equivalent to the upland 'Elm decline' recorded across Britain and Ireland. The age is later than those in the Manx lowlands, but the radiocarbon age of ca. 4800 ¹⁴C BP is consistent with ages in the nearby British and Irish uplands [104–107] where a similar upland-lowland age dichotomy of around half a millennium occurs (Figure 17).



Figure 16. Radiocarbon ages for the *Alnus* rise in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.



Figure 17. Radiocarbon ages for the *Ulmus* Decline in the northern Irish Sea region. For sources and date calibration ranges see Supplementary File S1.

Sporadic single grains of Tilia have been recognised in the Manx pollen assemblages but are not secure evidence that the tree might have been native to the island. Tilia is by nature a low producer of pollen and the grains are transported by insects and not by wind like birch or pine, and so *Tilia* pollen grains are often poorly represented in sediments. Isochrone pollen maps [2] show that the Isle of Man was on the latitudinal limit of the spread of *Tilia* across Britain and Ireland [108,109], reaching the shores of Lancashire ca. 6300 cal. BP. Coupled with a slow migration rate near the edge of its range in this region [2,86] this makes it likely that *Tilia* did not manage to reach the island. Pollen grains of the less common trees Fraxinus, Acer, Taxus and Fagus also occur in extremely low numbers, and rarely prior to the late Holocene disturbance of the woodland by humans. As the pollen percentages of these trees would be very low in any case, it is as yet not possible to say whether they were natural members of the Manx flora, although of these, *Fraxinus* is the most likely to have been so. It is present in percentages similar to those encountered in regions surrounding the Irish Sea basin, arriving at Montpellier Bog after 5000–4500 cal. BP (Figure 8) and is sparsely present at Quarry Bends after ca. 4000 cal. BP, with the clearest evidence at Greeba Curragh in the central valley where Fraxinus was reasonably abundant ca. 5800 cal. BP, and present at ca. 6700 cal. BP. Isochrone maps of tree expansion [2] suggest that Fraxinus reached the coasts of the Lake District and Lancashire

ca. 6000–5500 cal. BP, ages that are not dissimilar to the earliest occurrences of *Fraxinus* in Manx pollen records, and extended into Scotland after ca. 5000 cal. BP. Earlier arrival of ash is possible, and Manx native status is likely, although expansion would have needed a stimulus such as disturbance (see below). Isochrone maps of the expansion of *Fagus* across Britain and Ireland show that beech did not occur in the woodlands surrounding the Irish Sea basin in any numbers and was not present in any quantities on the Isle of Man, if at all.

5.2. Insularity

The land connection between the Isle of Man and Great Britain was finally broken when the postglacial eustatic rise in sea level submerged the low-lying land bridge between the island and England's Cumbria. Much deeper water lies to the west and north of the island, between it and Ireland and Scotland, respectively. The exact age of the severance remains uncertain, depending on which sea-level curve and model are considered. Lloyd et al. [110] present evidence for relatively high sea level (~0 m OD) along the west Cumbrian coast during deglaciation ca. 18,000 cal. BP, but this was followed by rapid relative sea-level fall between 18,000 and 14,500 cal. BP due to accelerated isostatic uplift. Hence, a postglacial land bridge might have developed in this window. For example, the Bradley et al. [111] relative sea-level curve has relative sea level below -20 m OD between 17,000 and 14,000 cal. BP. However, it is clear that eustatically driven sea-level rise became dominant as uplift rates decreased and severance of the island occurred around the time of the Lateglacial-Holocene transition (~10,500 to 9000 ¹⁴C years ago [48,112–114]. This is further supported by Huddart et al. [115] who dated thin basal peat beds at around 16 metres below sea level in Morecambe Bay, between north Lancashire and southern Cumbria, to centuries after 9000 ¹⁴C BP. If the Isle of Man was connected to Britain for up to a thousand years at the start of the Holocene there is no reason why most of the major forest trees would not have colonised the area that would become the island, even in very low populations to start with [116]. Even if the land bridge had not existed, however, the ability of tree and shrub propagules to cross bodies of water is remarkably high, and the distance from the island to Cumbria, only 66 kilometres, would have been easily crossed at any time in the postglacial using vectors such as birds and sea currents. Insularity has been considered as a reason for the late pollen rise of trees on other large islands off the western British coast, for example *Corylus* on the Isle of Arran in south-west Scotland [117] but has been discounted as similarly late pollen changes occur in places on the British mainland where insularity was not a factor. The presence of all the major Holocene forest trees in Ireland, which might or might not have ever had a land bridge to Britain [112,118], indicates the ease with which tree propagules can cross seas [17], delivered by currents or birds. Native Juniperus and Betula occur on far more remote islands than the Isle of Man, such as Iceland [116], indicating that insularity would not have been a significant factor [119] in the dispersal of trees to the Isle of Man.

There is strong macrofossil evidence in both Britain and Ireland that particular forest tree taxa were present in places long before their pollen frequencies rose to their rational, or even their empirical, limits. Froyd [120] discovered *Pinus* stomata preserved in lake sediments in northern Scotland that date to almost two thousand years before the major increase in *Pinus* pollen frequencies in the sediment profile, as did Fossitt [121] in northwest Ireland. *Alnus* macrofossils have been found in Lateglacial sediments in north-east England [16,122], and most significantly for early immigration to the Isle of Man, at Hawes Water near the coast of north-west England [123]. The regular recording of the pollen of temperate forest trees in Britain and Ireland well before their pollen becomes consistently present, even in Lateglacial contexts, need not represent long-distance transport or reworking of sediment, but records actual native presence, as suggested by Stolze and Moneke [124] for *Carpinus* and *Tilia* in their comprehensive study of Irish pollen diagrams. Alternatively, the recording of isolated pollen grains of a tree well before its consistent presence does not prove its local presence. Pollen percentage threshold values [125] might be a better indicator of tree presence, rather than single records, particularly for taxa with

poor pollen productivity or transport. On the Isle of Man, therefore, the single grain records for *Fraxinus*, *Acer*, *Taxus* and *Fagus* should not be taken as proof of presence. Regarding the native tree taxa, however, it is very likely that the arrival and establishment of all the major woodland trees occurred on the Isle of Man long before the expansion of their populations that is reflected in their rational pollen limit. Factors other than their age of immigration must have determined the time of their expansion on the island.

Although not a major barrier to dispersal, insularity, even on relatively large islands like the Isle of Man, can have environmental consequences including vulnerability to weather extremes throughout the Holocene, particularly Atlantic storms which can cause extensive treefall, as in Western Scotland or the Orkney Isles [126–128], particularly in upland areas. Such disturbance and the creation of gaps in the continuity of the forest would have provided opportunities for the colonisation and establishment of secondary tree taxa, as discussed below.

5.3. Climate

When the final Lateglacial stadial phase of severe cold (GS-1; Loch Lomond Stadial) terminated about 11,700 cal. BP and climatic amelioration then progressed during the early and then mid-Postglacial, climate change would have been the main driver and determinant of vegetation change, particularly among tree populations as successive types of woodland were established and replaced in turn. Although the substantial increase in temperature that brought the Lateglacial to an end in the Isle of Man was very rapid [129–131], there must have been significant delays in the response of vegetation to climate caused by the migration rates of different trees and the location of their refugia [132], as well as by the pace at which soils developed to support tree growth under the new climate regime [85]. The creation of a 'stable' mid-interglacial temperate Holocene forest would take thousands of years, such forest equilibrium not being achieved in north-west Europe until after about 8000 cal. BP [133]. Broadly, early and mid-Holocene climate has been divided into a 'Boreal' phase of warm and dry conditions between ca. $9000 \, {}^{14}C$ BP (ca. 10,100 cal. BP) and ca. 7000 ¹⁴C BP (ca. 7800 cal. BP) and an 'Atlantic' wetter and milder phase until ca. 5000 ¹⁴C BP (ca. 5800 cal. BP). There was no simple latitudinal 'wave of advance' of successive tree taxa [134,135] into Britain and Ireland, however. Although temperatures remained generally high until about 4200 cal. BP when major global cooling began [136], there were considerable climate fluctuations within the general early to mid-Holocene warming trend which greatly complicated forest development. These could slow or even reverse successions towards the naturally closed-canopy dense temperate deciduous forest [137,138] that categorises the 'mesocratic' phase of an interglacial [139], certainly in the Isle of Man where there was no question of any reduction in forest density [140] by large herbivore populations. These Holocene climate fluctuations included rapid changes to very cold phases that lasted a relatively short time [141] particularly around 9.3 and 8.2 cal. BP [142,143], but included other temperature changes of lesser severity, as well as phases of reduced or increased rainfall, due to cyclic climatic fluctuations in the Irish Sea region [144]. The two severe early Holocene cold events have been recognised in the oxygen isotope record in the northern Irish Sea region, as at Hawes Water in north Lancashire [145–147], and might have had impacts on the Isle of Man.

In places these severe climate events have been observed to have caused changes in woodland composition, temporarily reducing thermophilous tree taxa and promoting more cold-tolerant, open vegetation. The 9.3 episode (the Pre-Boreal Oscillation) has been observed to cause woodland recession in north-west Europe [148,149], particularly within areas newly colonised by postglacial woodland. The 8.2 vegetation reversion has been recognised as severe and long-lasting in both pollen-based and simulation studies [150,151] and has been noted in both Britain and Ireland (e.g., [152–154]) and in Europe (e.g., [155–159]). However, although high-resolution multi-proxy study of the 8.2 event in south-west Scotland [160], to the north-west of the Isle of Man, revealed woodland recession at this time, it might well have been as likely to have resulted from human activity as the effects of the colder climate. Vegetation change around that time cannot be assumed to have a climate driver, although that is almost certainly the likeliest cause of tree recession, certainly for the more thermophilous taxa such as *Corylus, Ulmus* and *Alnus*, as has been shown elsewhere in northern Europe [161], which would have been very sensitive to such short-term but severe climate events [162]. Although there are fluctuations in the tree curves on the Isle of Man pollen diagrams, there are no clear regressions towards more open vegetation or to peaks of more cold-tolerant trees that can be correlated with the time of the two early Holocene cold climate phases. Their effects were apparently not felt on the island, as is the case for many pollen diagrams in Britain and Ireland, perhaps because of its oceanic location [156,160]. There would have been a time-lag before tree populations responded to sudden climate deterioration [5] and severe but very brief cold phases might not have time to register given the sampling interval of most pollen diagrams.

Variations in rainfall also occurred during the early and mid-Holocene and these climatic fluctuations, although often short-lived, would have had significant influence on tree populations and distribution. The rise in Corylus pollen occurred during a period of generally warmer and drier climate [163] which would have favoured hazel expansion, both in abundance and range, as the Holocene thermal maximum ensued [164]. In the central Lake District in northwest England Pennington [165] noted increased pollen influx and in-washed mineral sedimentation ca. 7260¹⁴C BP, signs of increased rainfall at a time of raised water levels in the Cumbrian lakes and coincident with the age of the Alnus pollen rise. The *Alnus* rise [2,96,166] has long been attributed to the effects of a wetter, more oceanic climate and proxy data from several studies of bog development in the region have provided evidence to support a switch to wetter conditions around this time [163,167]. Some variability exists in dates for the Alnus rise, probably because of local factors causing very early establishment in places bordering the Irish Sea [168], but the correlation between wetter climate and the main increase of alder is compelling. There was also a pronounced shift to colder and wetter conditions from ca. 5900 cal. BP, recorded in ombrotrophic mires in the northern Irish Sea region [163,169–172] and in Irish lakes [144], coinciding with the centuries leading up to the Ulmus decline. As this period coincides with the adoption of agriculture on the Isle of Man, discussed below, it is possible that climatic stress might have played a role in prompting this cultural change in the western parts of Britain and Ireland [173,174]. The maps in this paper, that present the available ages for the main tree pollen rises, show that the range and average of the ages from *Corylus* onwards on the Isle of Man and in the neighbouring areas of Britain and Ireland are the same. This suggests that regional climate was the dominant factor in permitting tree expansions, although other, local factors might have been influential in deciding where expansion occurred, and at what scale.

5.4. Geology and Soils

Although climate was the macro-scale driver of regional changes in forest composition, secondary factors would often determine tree populations at the more local scale. Of these, geology substrate and the soils developed upon it was probably the most influential factor in the expansion of woodland and its constituents in any local area of the Isle of Man. The northern plain of the island, with a high proportion of light and unstable sandur soils, is the prime example, with vegetation successions retarded so that *Betula* woodland did not develop until the end of the first Holocene millennium, several centuries later than on heavier, more stable glacigenic soils in the neighbouring lowlands of Britain and Ireland. The similarity of the ages for the *Juniperus* peak on the sandur plain of the Isle of Man and on the redistributed fluvioglacial coversand area of southwest Lancashire [175,176] noted above must reflect similar delayed successions on unstable, sandy glacial outwash soils. An age of 9120 \pm 60 BP [10,338 cal. BP] for a peat at Holiday Moss within coversand in southwest Lancashire [177] which has a pollen assemblage dominated by grasses, sedges and ruderal weeds, shows that unstable sandy soils were unable to support *Betula* woodland for the first Holocene millennium, as was the case in the northern Isle of Man. Late rational

limits for deciduous trees at the only Manx early Holocene upland record at Montpellier Bog will have been caused by exposure to the colder upland climate and the thin acidic upland soils [40], and are not dissimilar to some ages in nearby upland Britain and Ireland. Migration routes and rates after first establishment are also likely to have been heavily influenced by soil characteristics, the spread of *Pinus* from southern to northern Ireland being a good example [17], where pine avoided the heavy, base-rich soils of central Ireland, which were dominated by *Corylus* colonisation, and spread up the west and east coasts of the island. When a climatic threshold had been passed for a rapidly migrating taxon such as *Corylus* therefore, it may well be surficial geology and pedology that are the limiting factors for tree species expansion after establishment, as Theuerkauf et al. [178] found for *Corylus* in the early Holocene of north central Europe, where dry, fine-grained and sometimes unstable soils prevented the establishment of deciduous tree cover in a similar way to the Manx northern plain. Similarly, limestone soils would have favoured the expansion of *Ulmus* in areas such as western Ireland [103] or south-east Cumbria [179], where Birks [180] noted the high mid-Holocene pollen frequencies of calcicoles *Ulmus* and *Fraxinus*.

In many cases, therefore, edaphic controls would have been the main regulator of woodland composition on the Isle of Man. The expansion of *Alnus* is a good example, when increased climate wetness produced waterlogged soils in 'Curragh' wetlands, topographic basins in the island's northern plain and in alluvial areas of the central valley [72]. At its rational limit *Alnus* replaced *Salix* and *Pinus* in these areas, and not only expanded but became abundant, as at Quarry Bends and Ballaugh Curragh 21, dominating the pollen assemblage with high production of local pollen from trees on and fringing the wetland basin. At non-Curragh sites the *Alnus* expansion occurs but is much more moderate. While climate would have been permissive in allowing expansion of particular tree taxa, edaphic factors would have controlled the distribution and abundance of expanding tree populations.

5.5. Competition and Tree Spreading

Climate changes were the main permissive factor driving the early and mid-Holocene expansion of various tree taxa on the Isle of Man, and geology and edaphic conditions were the primary factors in controlling the timing and location of the spreading of particular taxa within the forest community. Other secondary factors also had a significant influence, however, one of which was competition between established forest components and potential colonising taxa. For many tree species finding a niche within the established woodland, and then expanding from it, is not easy, particularly in later deciduous forests which cast heavy internal shade. Many trees have to be opportunistic after their initial colonisation, when conditions are not yet suitable for their general expansion through the landscape, like *Pinus* in Ireland [181]. Alnus, for example, which became abundant in the mid-Holocene, is a poor competitor and needs a stimulus like fire to destabilise the woodland [182] or a wetter climate [96] to provide opportunities to enter the forest and expand its populations away from its specialist niche. Once tree populations became established on the Isle of Man there would have been significant competitive interactions [183,184] between individual taxa, both during spreading but also once the mature forest matrix had formed, and these are reflected in the pollen record [185] which allows the reconstruction of forest structure [186], although longer-tern successions may need the use of fine-resolution palynology [187]. Holocene climate changes generally occurred slowly, however, so that the response of the woodland to climate change was tempered by intra-community ecology [184,188], with inter-specific competition and interference having major influences depending on local, mainly edaphic, factors. Examination of the Isle of Man tree pollen diagrams shows that once a colonising tree species had entered the forest and found its optimum population, there was little variation in the proportions of the arboreal components of the forest as equilibrium was achieved and maintained for long periods of time [135]. There is considerable stability, inertia and resistance to change in forest ecosystems [189–191], with autochthonous successional changes amongst long-lived forest trees taking centuries, with

senescent individuals or those killed by insect or fungal pathogens [101] usually replaced by members of their own species unless large numbers of individuals were affected, when community destabilisation could occur and the woodland structure changed, perhaps as at the *Ulmus* decline [98]. Disturbance, by natural or human agency, might well have often been the trigger for the promotion of diversity and community change within the woodland, in the Isle of Man as elsewhere.

5.6. Disturbance and Human Activity

Any external disturbing force that breaks the inertia and stability of the forest is likely to provide opportunities for woodland taxa that are locally present but uncommon to expand their populations, finding a newly opened area into which to spread. This is particularly so for any woodland trees and shrubs which are rapid colonisers and grow quickly to maturity and which can take advantage of their membership of the seral regeneration process as woodland becomes re-established, allowing their expansion from niche habitats to a major role in the restored forest matrix which they then retain. Significant disturbance might therefore permit the local expansion of a tree or shrub earlier than would have occurred autogenically, perhaps much earlier, causing a permanent change in the forest ecosystem and reduction in the populations of the previously established dominant woodland trees. This process and changes in tree abundances will be reflected in Manx pollen diagrams and, along with edaphic and other factors, might explain the earlier ages (Table 1) for some pollen zone boundaries on the island. There are various mechanisms by which disturbance can come about, including natural factors such as major storms [128] which can result in windthrow and landslide. Specific occurrences of such factors are difficult to recognise in the environmental evidence however, although phases of unstable atmospheric conditions during which such severe storms were more likely can be identified in the climate record. Barclay et al. [192] have suggested exposure to high westerly winds as a likely cause of woodland decline in late prehistoric times in upland western Scotland in the absence of anthropogenic influences, as have Birks and Madsen [126] in the western Scottish islands. Allen [193] has shown that most tree trunks preserved in mid-Holocene sediments show evidence of having been wind-felled, on a range of criteria, are aligned west–east and can be correlated with strong, probably gale-force westerly winds during that period. Sacheverell [194] mentions that great tree trunks discovered at depth in the peat of the Isle of Man's Curragh wetland were all aligned in a north-easterly direction. Wind-throw during westerly storms is likely to have been the cause and would have been a major cause of tree felling in the exposed Manx island landscapes of the early to mid-Holocene, particularly in the uplands.

Fire is a major disturbing force in woodland and can operate at various spatial scales depending on its ignition source and the inherent flammability of the woodland matrix in which it occurs. It can have a natural origin through lightning strike, although the recurrence interval of lightning fires and their ability to take hold in an oceanic, wet climate like that of the early and mid-Holocene Isle of Man was probably low. A more likely trigger for fire disturbance on the island during the first half of the Holocene, when the forest matrix was being assembled and pollen zone changes were occurring, might have been human agency. Fire in the hands of Mesolithic hunter-gatherers can be a very potent force for vegetation change, especially if applied to the forest in any systematic way [195–197], but even as an occasional escape from domestic hearths and campfires [198]. Deliberate burning of woodland by Mesolithic people to create open areas, thus increasing yields of vegetable food and encouraging game populations [197] seems likely in areas of the British uplands where the evidence for systematic burning is strong [199,200]. Such purposeful environmental niche construction by foragers [201] seems less likely in the Isle of Man, despite archaeological evidence for a substantial Mesolithic occupation in the island from the early Holocene onwards [202,203], as native large game animals were almost certainly absent in the early to mid-Holocene [37], as they were in Ireland [204]. The increased yield of many vegetable foods, particularly hazel nuts, during regeneration after fire would still

have remained a persuasive motive for fire-starting. Hunter-gatherer use of fire can cause long-lasting changes in woodland structure [205], with rapid-growth, early coloniser trees like *Betula* [206] assuming local dominance as a stage of woodland regeneration, as can be seen in some Manx pollen diagrams.

There are few examples of such Mesolithic disturbances at Manx pollen sites, although low levels of charcoal are consistently present in some diagrams, as at Greeba Curragh. At Ballachrink LT12, however, at 6925 ± 55 BP (7793 cal. BP) there is a clear phase of local burning, with a peak of microscopic charcoal and a sharp reduction in Alnus pollen frequencies, as well as those of Corylus, Quercus and Ulmus. Poaceae and Pteridium values increase and weeds of open ground appear in the pollen record in a phase of woodland canopy opening by fire. Although this fire-disturbance is clearly after the Alnus rise at this site, lower in the same profile the rises of *Quercus* and *Ulmus* pollen frequencies and reduction in *Corylus* coincide with a high peak of charcoal, so that fire may have played a role in breaking the dominance of the hazel thicket and allowing the local colonisation of oak and elm. There is also a major charcoal peak across the Alnus rise age of 7370 ± 35 BP (8175 cal. BP) at Quarry Bends, and this association of fire with the expansion of alder is a feature noted on many pollen diagrams in Britain and Ireland, including in all of the areas bordering the northern Irish Sea (e.g., [107,207–209]). It is possible that the forest opening caused by fire could have given alder the opportunity it needed to enter the woodland matrix and locally expand its population. The relatively early age at Quarry Bends for alder expansion indicates that fire destabilisation of woodland probably allowed alder to spread earlier than it would otherwise have done. Fire disturbance has been recorded towards the end of the Mesolithic cultural period at Ballaclucas (LT5) in the northern Lhen Trench, an area with many Mesolithic flint sites [210], at 5990 \pm 55 BP (6815 cal. BP) with the replacement of *Alnus* and *Quercus* woodland by secondary trees and open ground weeds [48]. An almost contemporaneous and similar fire disturbance event occurred at nearby Ballachrink (LT12) at 5925 \pm 60 BP (6750 cal. BP), this time with cereal-type pollen as part of the post-disturbance herbaceous pollen assemblage [57]. If this pollen grain is really an indicator of cultivated cereals, the transition to the Neolithic must have started early in the Isle of Man. Earlier Holocene fire disturbance could, of course, have had a natural origin, particularly during drier climatic periods, and its attribution to human agency must remain circumstantial [211]. On the whole, although hunter-gatherer communities might well have caused small and localised changes, the Holocene history of the lowland vegetation in the Isle of Man before the Ulmus decline was dominantly that of the natural spread and development of forest.

The Ulmus decline occurs during a phase of deteriorating climate, discussed above, and might well have been multi-phased and multi-causal [102] but the often direct association of this pollen-stratigraphic feature with pollen evidence of ruderal and open ground weeds, notably Plantago lanceolata, that indicate forest opening in most regional pollen diagrams suggests that human disturbance was most often the cause of the fall in *Ulmus* populations, particularly as the feature often coincides with the presence of radiocarbon-dated early Neolithic archaeological sites [212,213]. Land-use by early Neolithic farmers [214]), immigrants to the island via Irish Sea maritime connections [215], that focused on elm trees seems most likely, particularly as cereal-type pollen was sometimes part of the disturbance pollen assemblage across the Ulmus decline in all regions adjoining the northern Irish Sea [216–218]. The creation of small, cleared areas within the forest, sometimes employing fire but perhaps also through girdling and leaf-stripping of elm trees [219] and the browsing of livestock [220], would produce the pollen signal recorded [197,211,221]. Ages for earlier Neolithic sites on the Isle of Man [212,222,223] provide a broad chronological association between the elm decline and the start of forest farming on the island. Although factors including climate and disease might have contributed to the multi-phase decline of elm populations [224], as elsewhere in the wider region, it was the introduction of Neolithic pastoral agriculture, with small-scale cultivation, that probably caused the Ulmus decline

on the Isle of Man, which most likely records focused human disturbance of the island's mixed deciduous forest [225].

6. Conclusions

Comparison of published radiocarbon ages for early to mid-Holocene pollen zone boundaries in the areas of Britain and Ireland that are adjacent to the northern Irish Sea, based on high amplitude changes in the frequencies of the major woodland trees, has shown that there is great similarity in the average age for the expansion (the rational pollen limit) of each successive tree taxon throughout the region. There is, however, a considerable range of ages, amounting to several centuries, around the average time of expansion for each tree species in each area. While Holocene climate change is likely to have been the main driver for the successive expansion of each tree species' population after establishment in the landscape, and therefore of their rational pollen limit, the ranges in the ages will have been caused by local secondary factors including geology, altitude, pedology and disturbance which will have promoted or delayed the expansion of particular tree species. Long 'tails' in the tree pollen curves on diagrams before their rational limit suggest that most tree taxa had arrived in each region in small numbers well before their expansion to high populations when climatic factors became conducive.

The situation on the Isle of Man was very similar, with individuals of most tree species likely to have arrived in the island in the earliest Holocene before its separation from Britain, so that insularity was not a major factor in the composition of the island's woodland. Ages for the expansion of almost all Holocene tree species are the same as those in Britain and Ireland, including the range of ages, indicating that a regionally operating factor, climate, was the driver of woodland change across the whole of the northern Irish Sea region. The major exception is in the first Holocene millennium, when the expansion of Juniperus and Betula was delayed by several centuries on the Isle of Man compared with ages in adjacent areas of Britain and Ireland. This discrepancy, with a prolonged period of Manx pre-woodland vegetation, would have been due to edaphic factors caused by the glacial legacy of the northern plain of the island, where most radiocarbon-dated sites occur. More stable pedological conditions later in the Holocene brought Manx lowland woodland evolution into line with Britain and Ireland. Delayed rational limits of thermophilous trees are also apparent at Montpellier Bog in the Manx Uplands but are broadly comparable to the British and Irish upland situation, where exposure and thin acidic soils also made deciduous tree colonisation difficult. Human and other disturbances occurred on the Isle of Man and would have had a similar degree of influence on woodland history as on the two neighbouring major islands, often providing opportunities for early colonisation by new tree taxa. While climate was the long-term regulator of woodland composition on the Isle of Man, there is no real evidence in the pollen data that the sharp cold phases of the earlier Holocene caused any regression in woodland development, perhaps because of the island's maritime situation.

A final conclusion is that the use of isopollen maps for a small area, such as the Isle of Man, would not be warranted as local, secondary factors will have caused great variability in the timing of pollen assemblage changes, superimposed upon the influence of long-term climatic change. The temporal and spatial resolution of isopollen maps is inevitably coarse and they should be reserved for large scale reconstructions of climate and forest history, based on representative sites that were unaffected by local factors which might have amplified or mitigated the effects of climate.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/quat6010003/s1, File S1: References for Figures 10–17.

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