PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

History of the Natural Forests of Britain: Establishment, Dominance and Destruction

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History of the natural forests of Britain: establishment, dominance and destruction

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The Cambridge data-bank of Quaternary fossil plant records has been used to derive an objective outline account of the chief British forest trees through the Flandrian Period, i.e. the last 10000 years. Their history is evidently related to the climatic pattern of an uncompleted interglacial cycle, showing response to pre-temperate, early-, middle- and late-temperate stages and passing through phases of establishment and dominance before becoming subject to the destruction initiated by Neolithic man about 5000 years ago and disastrously accelerated afterwards.

The native birches and pine were essentially protocratic: pine, established abundantly through south and east England in the first two or three millennia gave place to the mediocratic elm, oaks and limes dominant thereafter, save in Highland Scotland where pine forest, established late, continued as climax community. Beech and hornbeam, telocratic in character, spread only in the latest millennia, possibly in relation to relaxation of clearances but possibly also in relation to altered climate.

Introduction

The value of a survey of British forests through the last 10000 years lies, first, in the possibility of showing what our natural forest cover would have been in the absence of the progressive disforestation and exploitation of the last five millennia, and, secondly, in the indication it may afford of the climatic, edaphic and biotic factors that have determined the natural distribution of our native trees and of the communities they have constituted.

The evidence employed is that of subfossil material found in contexts to which at least an approximate date can be assigned, either macroscopic remains such as timber, charcoal, fruits and flowers, or the far more abundant microscopic pollen that is shed in vast amounts and is stratified into accumulating deposits of peat-bogs and lake-basins. Records of both types are stored in the data bank of the Sub-department of Quaternary Research in Cambridge, from which they have been extracted for the purposes of this survey.

We work with the advantage of a recently and greatly improved knowledge of geological, climatic and archaeological events of the whole Quaternary Period and in particular of the later part of it, and it is this that provides us at once with a background against which to see our forest history and a quasi-chronological scale by which our biological records can be brought into correlation.

The Quaternary Period comprised a sequence of alternate cold and temperate climatic episodes. The former induced in northern and temperate latitudes and at high elevations glaciations of large dimensions and great biological significance. In Great Britain glaciers extended at their maximum into southern central England and the Scilly Islands and over most of Ireland. It is hard to believe that any trees save perhaps birches survived in this country south of the ice. The intervening mild 'interglacial' periods, that lasted each a few tens of thousands of years, experienced a cycle of development in which soils and vegetation together

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responded to the overall control of climate as it moved towards a thermal maximum and then declined as the next glacial period approached. In a very condensed form we may represent the sequence as follows. After the cryocratic conditions of the glacial episode with its unleached, frost-shattered and disturbed soils and open dwarf vegetation, in these latitudes we have:

(1) a *pre-temperate* (*protocratic*) *zone*, with invasion by boreal trees such as *Pinus* and *Betula*, bringing increasing shading and root-competition and deepening of soils that increase in humic content;

(2) an *early-temperate* (*mesocratic*) *zone*, with deciduous mixed-oak forest (typically *Quercus*, *Ulmus*, *Corylus*, *Alnus*, *Fraxinus* and *Tilia*) upon rich brown-earth forest soils;

(3) a *late-temperate* (*oligocratic*) *zone* in which the soils become progressively podsolized and correspondingly the mixed-oak forest declines in face of expansion by *Carpinus*, *Abies*, *Picea* and *Fagus*;

(4) a *post-temperate* (*telocratic*) *zone* in which continuing decline of temperature and progressive soil degeneration are associated with forests of boreal trees, especially *Pinus*, *Betula* and *Picea* in stands becoming broken with damp ericaceous heath.

A cycle of this pattern has been clearly demonstrated in the three latest completed interglacial cycles in the British Isles and there is every reason to suppose that it is operating within the Flandrian Period, that still uncompleted interglacial episode in which we now live, and to

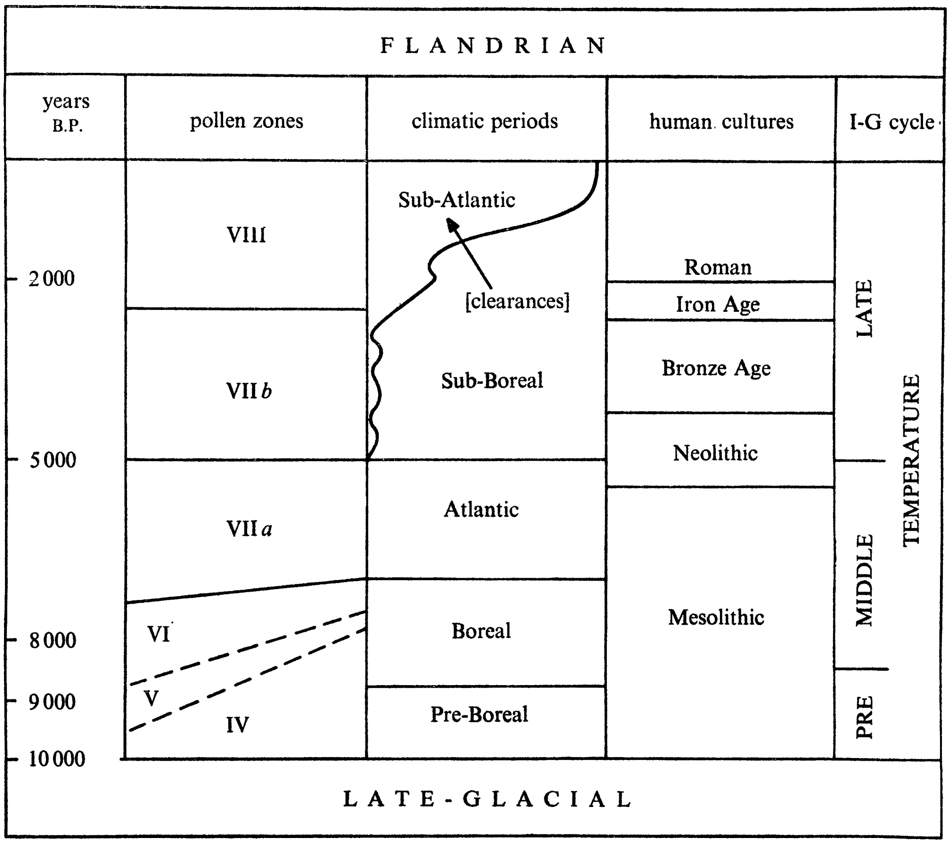

FIGURE 1. Schema illustrating the correlation of the pollen zonation employed in this paper (figures 2–11) with radiocarbon dates, climatic and archaeological periods. It represents the progress of disforestation since the early Neolithic and the presumed correspondence with the pattern of interglacial substages. The non-synchroneity of the early pollen-zone boundaries in different parts of the British Isles is indicated by their slope.

which it seems appropriate to limit this present survey. Rather arbitrarily we take it to have begun 10000 years ago, so that its events fall easily within the scope of radiocarbon dating, a method now extensively applied to all problems of Flandrian sequence and correlation.

After a modest oscillation between 12000 and 10000 B.P. it seems that climate rather swiftly improved and temperatures rose to a 'hypsithermal' interval, culminating between 7000 and 5000 B.P., during which mean summer temperatures were higher by 2 or 3 °C than those of today, and thereafter temperatures have fallen, certainly not uniformly and probably with changes also in 'oceanicity'. Sea-level, lowered by locking up of water in the ice-sheets, was progressively restored and the North Sea, still dry around 9000 B.P. had virtually reached its present dimensions by 5000 B.P. The Flandrian included the human cultures from the Mesolithic onwards: men of the Mesolithic Age were sheltered and supported by the natural forests, but from early Neolithic times, about 5000 B.P., men progressively destroyed them. Their settlements commonly have identifiable wood or charcoal remains. Before radiocarbon dating the most generally available Flandrian chronology was provided by pollen analysis. It depended upon the climatic progression we have described having induced a sequence of major vegetational changes of such consistency across the country, that with a good network of sites equivalent pollen assemblage sequences could be recognized. Thus there were set up numbered zones III–VIII with a major division of zone VII into two, covering the last 10000 years. The absolute chronology attributed to these zones was largely inferred by reference to the Swedish varve chronology, and with the advent of radiocarbon dating has proved remarkably close to the truth. The method, however, was very hard to apply to Ireland and Northern Scotland, and to the later part of the record when human activity heavily operated. It has proved also that to some degree the pollen zone boundaries are diachronous. None the less, so much of our collected evidence comes from pollen analyses made before radiocarbon dating, that our only practicable plan has been to organize the data in terms of the consecutive pollen zones, the shortcomings of the method kept, however, in mind.

So far as one here presents the data it is in the form of distribution maps in which spots represent for a given genus of tree the frequency of its pollen as a percentage of the total tree pollen (sometimes with symbols indicative of macroscopic finds) in given zones. When sites have been numerous it has been possible to make isopol maps for the zones. Both map types need very careful recognition of their basic limitations, especially the derivation from percentage totals, the danger of absence of sampling from some large tracts of country, such as midland and southern England and the diachroneity error mentioned already.

We consider the individual tree genera in the rough order in which they have come to prominence: a minimal correlation table is given to facilitate recognition of the zone sequence, etc.

Betula pubescens and *B. pendula* (tree-birches)

There can be no doubt at all that throughout the Flandrian Period tree birches have been present abundantly in all parts of the British Isles. That they were present also in the preceding Late Weichselian is proved by macroscopic remains and high pollen frequencies, especially in the milder Allerød interstadial (zone II) (figure 2), during which open birch woods occurred throughout western Europe. In the Late Weichselian *B. pubescens* seems to have been much the commoner species, but it is lacking in highland and western Scotland, where there is the more northerly *B. pendula*, a species that occurs, however, also in England, though not so far recorded at this time from Ireland.

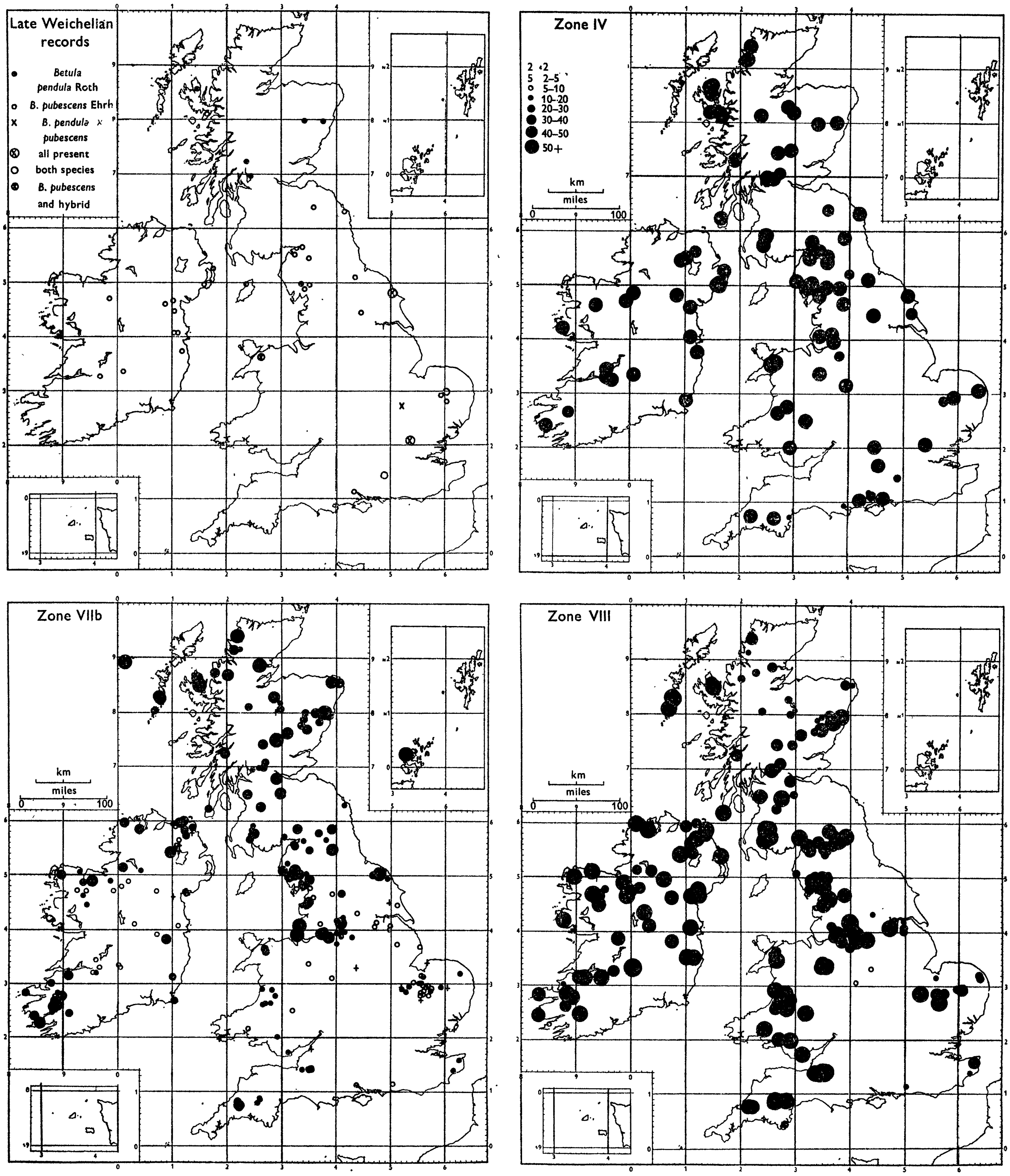

FIGURE 2. *Betula* spp. Records of macroscopic identifications of two species of tree-birch, *B. pendula* Roth. and *B. pubescens* Ehrh., and the presumed hybrid between them, from the Late-Weichselian: spot maps of the genus for zones IV, VIIb and VIII, indicate the relative frequency of birch as percentage of total tree pollen.

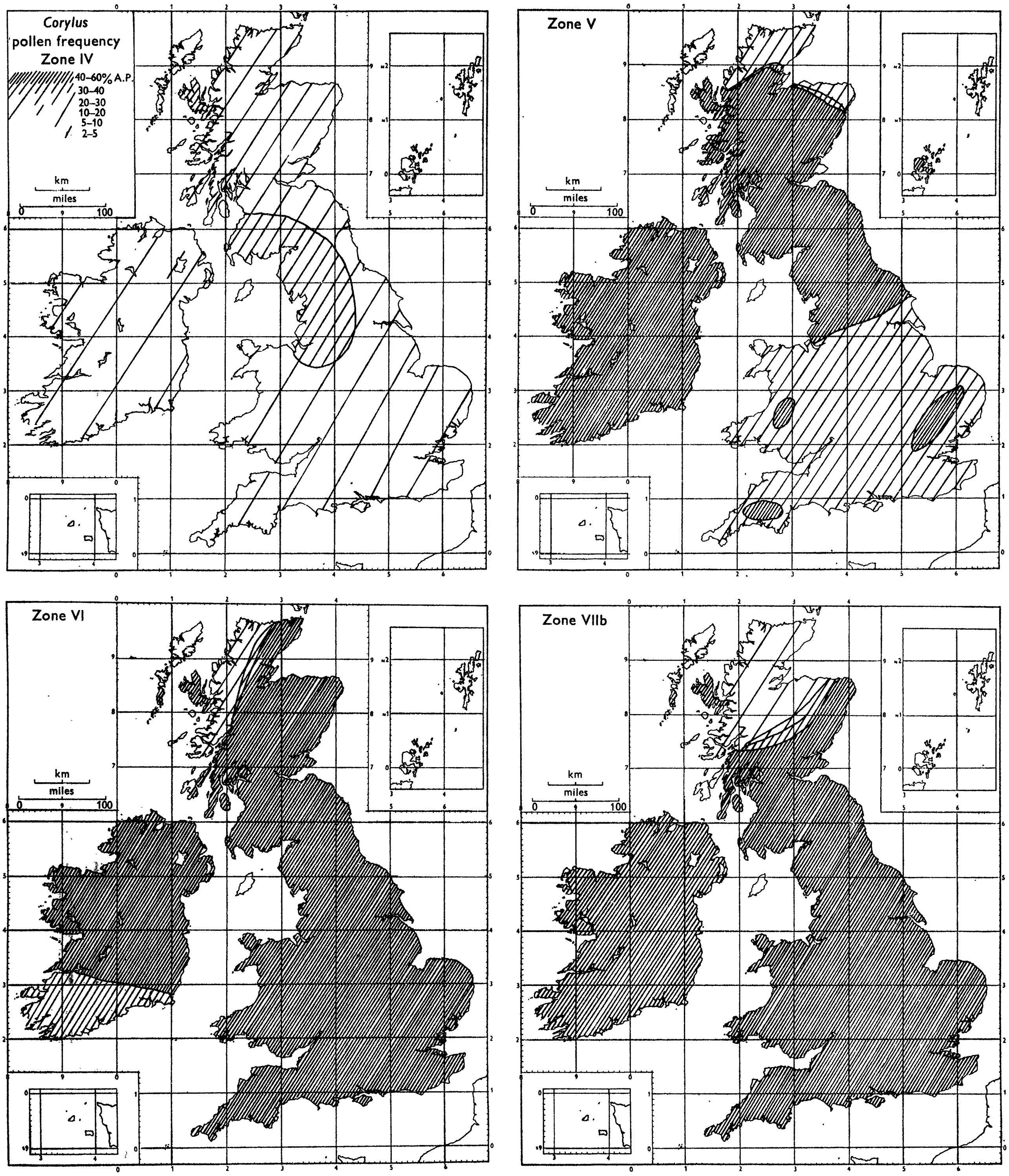

Figure 3. *Corylus avellana* L. Isopol maps of the hazel for zones IV, V, VI and VIIb, indicating ranges of frequency of hazel as percentage of total tree pollen.

The opening Flandrian (zone IV) was marked by a rapid spread of birch woodland throughout the British Isles, when it was often associated with juniper and willows. Birch wood continued to be generally abundant in zone V everywhere except in the region of pine forest of southeastern England. In zone VI it appears that high birch pollen frequencies were now absent southeast of the Scarborough, Brecon, Lyme Bay line (presumably because of the dominance of mixed-oak woodland with hazel and the continuing abundance of pine) and from all central and western Ireland (reflecting the continued importance of pine with substantial spread of oak, elm and hazel).

In zones VII a and VII b, tree birches continued important and no doubt substantial forest components throughout northern England and the whole of Scotland, both in the mixed oak forest area of central and southern Scotland and (to a less extent) in the area of the now established Caledonian pine forest. Some local increases in birch pollen frequency after zone VII a are certainly the reflexion of lightening of forest cover by the Neolithic and subsequent forest clearances that gained momentum from 5000 B.P. onwards. This is certainly in large part the cause of the very high frequencies of birch pollen in the Sub-Atlantic period (from *ca.* 2500 B.P.) save in the area of continued dominance of Scottish pine forest. The birch here has of course behaved as a seral element, rapidly recolonizing cleared and felled areas save where this was followed by intensive grazing or cultivation.

Corylus (hazel), figure 3

Representation of the hazel (*Corylus avellana*) in pollen analyses through the Flandrian presents a singular difficulty in that, for the early zones when it must have occurred in hazel-dominated communities it has every claim to be reckoned as part of the total tree-pollen scene, while in later zones it must have been to a large degree present as a shrub beneath the canopy of the deciduous forest, and as such, better reckoned outside the total arboreal pollen scene. We have adopted the former convention despite the fact that it conceals the very high Boreal frequencies of hazel in relation to forest trees and despite a degree of insensitivity that it imposes on the percentages of all other genera.

In zone IV immediately at the opening of the Flandrian period we find *Corylus* present in very substantial frequencies in Syke (where the age is confirmed by radiocarbon dating) and in sites on both sides of the northern basin of the Irish Sea: though macroscopic evidence is absent there can be no doubt of the actual presence of hazel scrub in these western sites (along with the prevalent tree birches) and it was probably present locally also throughout the rest of the British Isles. Individual pollen diagrams now register in zone V such tremendous and sudden increases in hazel pollen frequency as often to make it exceed several times the total of all other tree pollen: this phenomenon extends through the first part of the following zone VI. This is the Boreal expansion of hazel similarly noted on the western continental mainland (then in dry land continuity with the British Isles) and there seems little doubt that at this time it must have formed vast stretches of hazel scrub. It is not clear how far it may at this time also have been the undergrowth of pine forest: lower frequencies in southern and eastern Britain *may* possibly be associated with the prior establishment of pine woods there.

In zone VI high hazel frequencies obtained even in the Scottish Highlands and Caithness, but in the following zones it greatly diminished there, perhaps in association with the dominance of pine forest, and perhaps also in response to progressive podzolization. Over the rest of the British Isles the hazel continued a substantial contribution to the pollen scene, no doubt since it behaved as a stable undergrowth of the mixed oak forests, flowering freely on margins and temporary openings. It certainly responded in this way to temporary forest clearances by prehistoric man, and we have evidence from Neolithic time onward, that he made use of hazel coppice. Perhaps the violent large fluctuations in hazel pollen frequency seen in many pollen diagrams reflect these practices.

In zone VIII, the Sub-Atlantic period, while the great forest clearances extended rapidly throughout the British Isles, the general distribution pattern of hazel frequency was retained, but the percentage representation in relation to the tree pollen scene consistently fell, possibly because of the greatly increased representation of tree-birches and partly because of the decreased opportunities for hazel to flower in managed woodland.

Pinus sylvestris (pine), figure 4

Although there are strict limitations on what may be deduced from isopol maps, they allow nevertheless some generalizations of great interest. It appears that:

(1) In zone IV, say 10000–9000 B.P., pine was well established in southern and southeastern England, a view confirmed by identification of macroscopic remains in this area and consistent with the mainland European evidence.

(2) In zone V, pine was abundant in England southeast of the Tees, Brecon, Lyme Bay line, with indications of separate expansion in northern Scotland and western Ireland.

(3) In zone VI, pine had become abundant over all England and Wales save the southwest and northwest, over all Ireland, especially the southern half, and over northern and northeastern Scotland. There was a gap in the pine forests – not subsequently filled – of some 150–300 km., i.e. the separateness of the Caledonian pine forests from those native to southern England is very ancient and there may be grounds for regarding them as somewhat separate in origin. It was not merely a dense oak woodland that separated the north Scottish from more southerly pine forest but marine incursion had almost met across lowland Scotland between the Forth and Clyde.

(4) In zone VII a, pine forest had become generally unimportant throughout England, Wales and lowland Scotland, but the area of its abundance had expanded in northern Scotland: in Ireland a general reduction had taken place but to a less degree than in England. The broad pattern established in this, the Atlantic period, persisted right through following zones. Thus the Caledonian pine forests have certainly existed for at least 8000 or 9000 years. In the last two millennia they seem to have withdrawn from extreme northeasterly Scotland in favour of birch.

(5) It seems probable that there has been at least local continuity of growth of native pine woods in Ireland, especially the west, through to historic time. Within England higher values for pine persisted in the southeast in zones VII a and VII b, as in the preceding zones, and it seems probable again that in regions of the Breckland, Weald and Hampshire basin, native pine has persisted to the present day, though of course much supplemented by planting, perhaps by continental stock, in the last few centuries.

This abundant pollen evidence, together with numerous dated discoveries of pine stumps *in situ*, must now surely dispose of the legend of the non-indigeneity of pine in England, Wales and Ireland.

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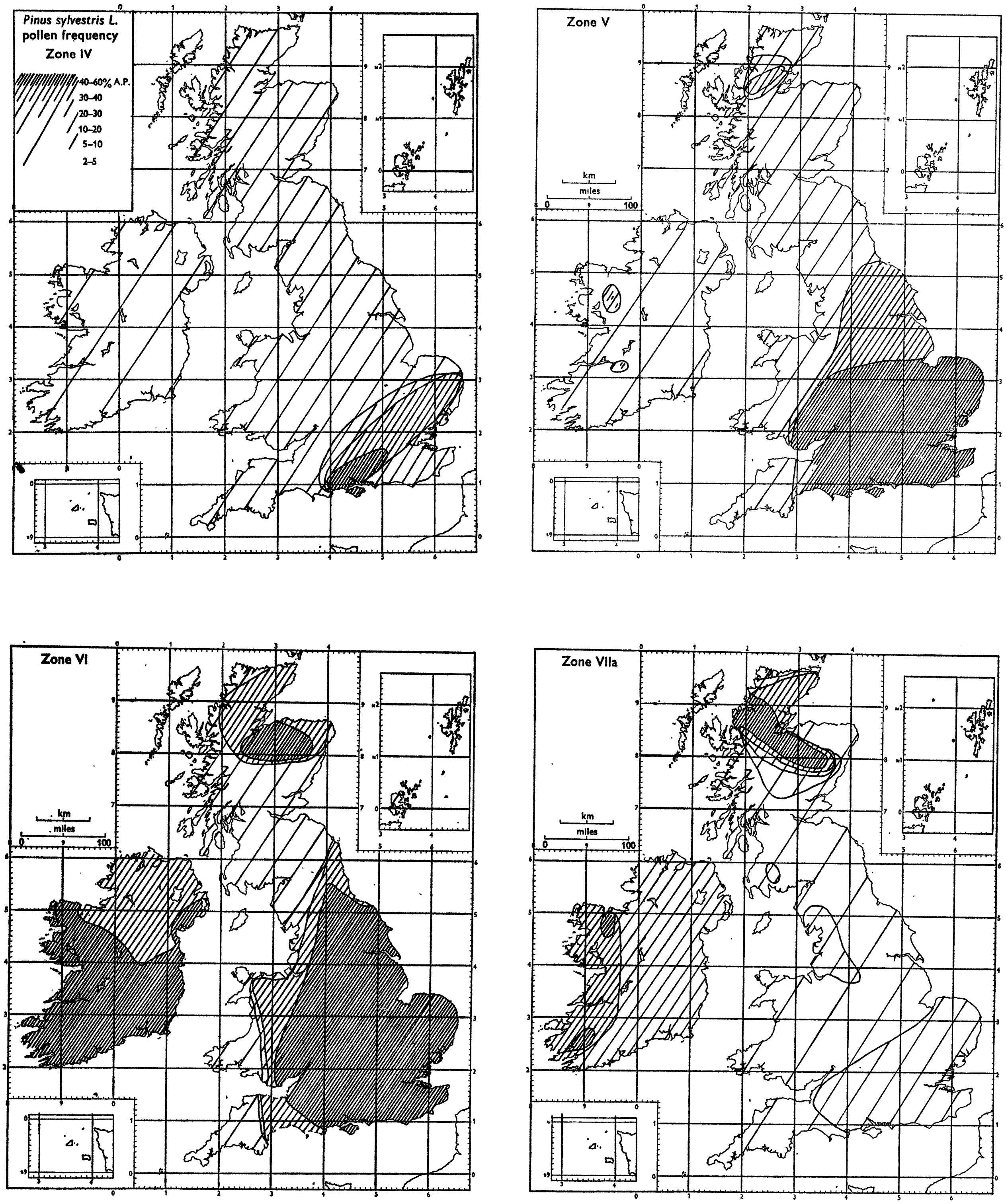

FIGURE 4. *Pinus sylvestris* L. Isopol maps of Scots pine for zones IV, V, VI, VIIa and VIIb.

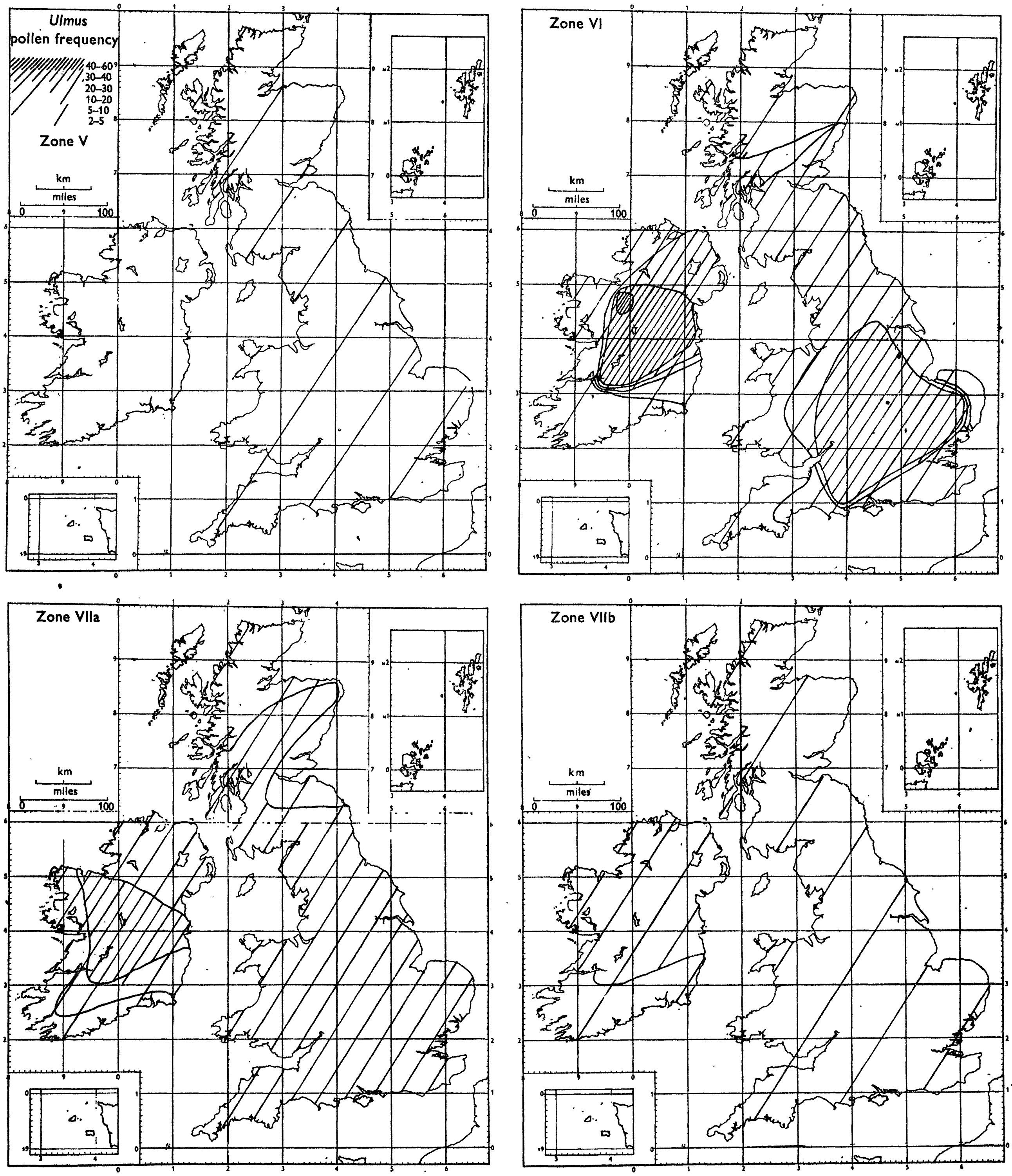

FIGURE 5. *Ulmus* spp. Isopol maps of the elm genus for zones V, VI, VIIa and VIIb.

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Ulmus (elm), figure 5

Certainly the principal and perhaps the only species of elm native in the British Isles is the Wych elm, *Ulmus glabra*: certainly it has a much more northerly and western range than the many other species or varieties now centred round eastern and southern England and it maintains itself in far more natural woodland communities than any of them.

In zone V elm pollen occurs throughout the British Isles in frequencies generally low but enough to indicate at least local presence, a condition indeed required to explain the wide dramatic expansion in abundance early in the following zone, where it commonly preceded that of oak. In Ireland mean pollen frequencies in zone VI equalled or exceeded those for *Quercus* and in the newly established mixed oak forest elm was everywhere important. In Scotland, where mixed oak forest was not at this time developed, elm frequencies had increased much less from zone V. In the succeeding Atlantic period (zone VII a) we need not suppose any great change in the status of elm though its pollen frequencies are lower since the mixed oak forest now also contains much local alder and, in England, a substantial percentage of lime (*Tilia* spp.). There has been some increase in elm frequency in southern and lowland Scotland, no doubt with establishment of mixed oak forest.

The opening of zone VII b was accompanied everywhere by very sudden and large diminution of the pollen frequency of elm and this has been shown by radiocarbon dating to be synchronous throughout the British Isles and beyond. It is strongly associated with selective suppression by early Neolithic man, initially for leaf-fodder (and subsequently, no doubt, by browsing, cultivation and grazing), but some climatic or other non-human biotic control may also have operated. The 'elm decline' has naturally become a horizon of great importance to palaeoecologists and archaeologists throughout western Europe. From this decline the elm seems never to have had chance to recover and its Sub-Atlantic (zone VIII) pollen frequencies are little different from those of the preceding sub-boreal (VII b).

Quercus (oak), figure 6

Subfossil evidence that differentiates the two British species of oak, *Q. petraea* and *Q. robur*, is so slight as to be negligible and our account treats merely of the genus. Its early Flandrian history is similar to that of the elm: in zones IV and V its pollen is present throughout the British Isles in frequencies large enough to indicate local stands in favourable localities, but no closed woodland. Again as with elm, in zone VI (figures 5, 6) oak pollen is present at so many sites and in such amount that we must assume oak woodland (with elm) had become established generally throughout England and Wales and central and western Ireland. There are, however, two different centres of special abundance, one roughly centring on southwest England and southeast Wales and one on opposing sides of the northern Irish Sea. The succeeding Atlantic period (zone VII a) saw no great change in the frequency pattern, although in north-eastern England and southern Scotland there was establishment in lower frequency than further south. It looks as if mixed oak woodlands now grew in suitable sites around and within the Scottish highlands, where, however, pine or pine–birch woods seem to have been preponderant. The low values in Ireland may be associated with continued high abundance of elm, and in eastern England with substantial amounts of lime: in lowland England and Wales the alder was also now abundant.

The elm decline, that so strongly affected the opening of zone VII b, was associated in England

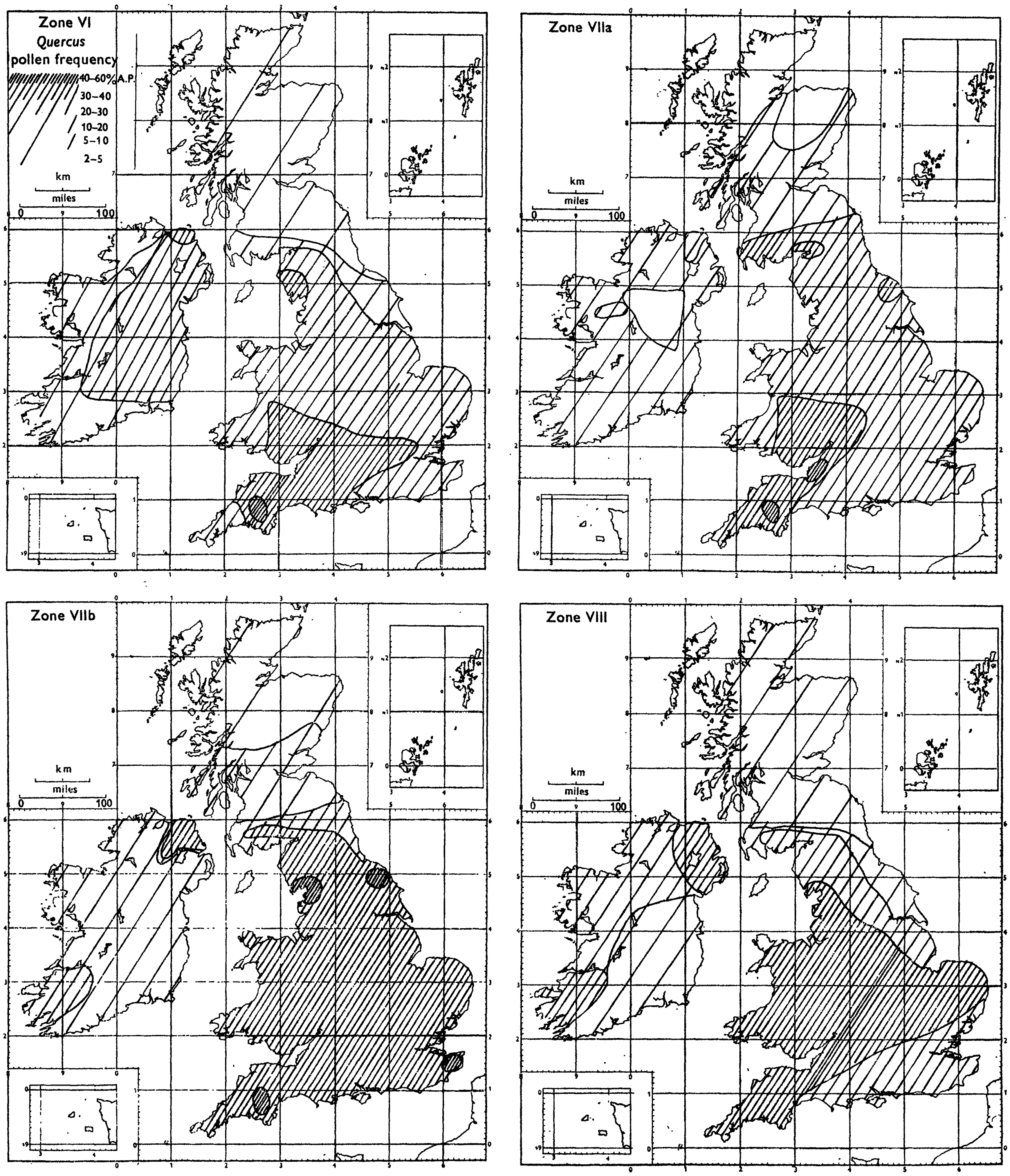

FIGURE 6. *Quercus* spp. Isopol maps of oak (*Q. robur* and *Q. petraea* unseparated) for zones VI, VIIa, VIIb and VIII.

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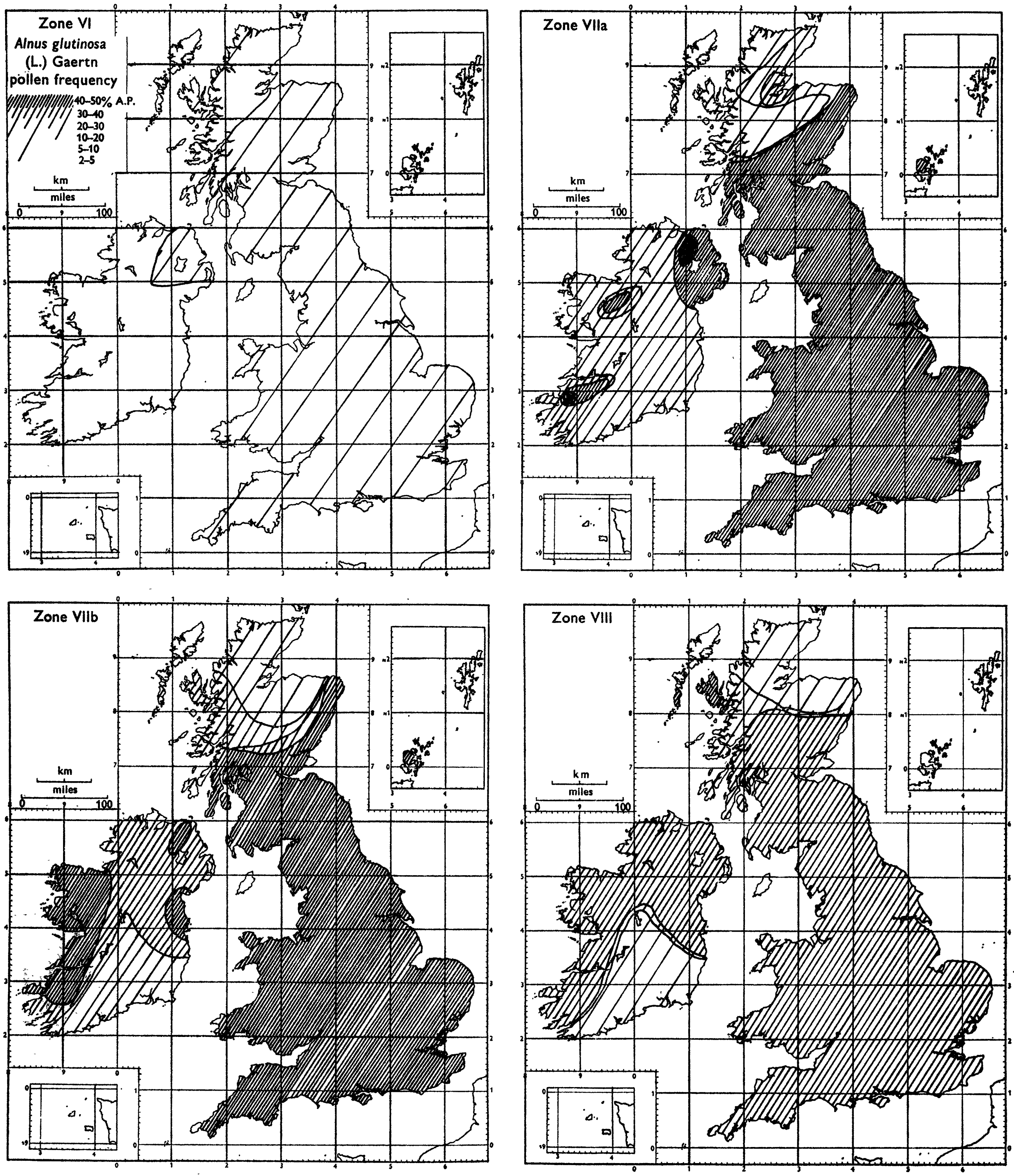

FIGURE 7. *Alnus glutinosa* (L.) Gaertn. Isopol maps of the black alder for zones VI, VIIa, VIIb and VIII.

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and Wales also with decreases in the abundance of pine and the lime, trees likewise subject to selective utilization, and this may account for the general increase in oak pollen frequency in these countries. Oak was not only tougher to fell but yielded a useful fruit crop if left standing.

The general frequency pattern was substantially unchanged in the Sub-Atlantic (zone VIII).

Alnus glutinosa (alder), figure 7

Alnus glutinosa, the black alder, is the only species of the genus recorded in the Flandrian history of this country. As with oak and elm, the distinctive pollen grains have been found at thinly scattered sites throughout the British Isles in zones IV and V, particularly the latter, in frequencies that indicate local presence of the tree in favoured localities: this is notably so in western Scotland (where *Corylus* had very early establishment also). During zone VI, however, especially the latest of the three subzones, at many sites it had reached substantial frequencies, particularly in northern England and northeastern Ireland (regions also associated together in the early establishment of oak and hazel). Now at the opening of the Atlantic Period (zone VII a) there occurred such a swift and permanent expansion in alder pollen frequencies that it seems only reasonably explicable as the consequence of climatic change to so much wetter conditions that existing woodlands now become diversified by local alder facies, in swales, stream and river banks and flood plains to such an extent that they took on a strongly mosaic quality. This rise in alder frequency was much slower in central and southern Ireland but elsewhere it strongly affected those areas bearing mixed-oak forest, i.e. broadly up to the Scottish highlands. During zones VII b and VIII there was no great alteration in the pattern of alder frequency save that in Ireland (excepting the south and east) it now approached the frequencies in Great Britain. Although unrepresented in the isopol map there was a pronounced increase identifiable in many individual pollen diagrams showing the response of the alder by quick re-establishment after forest clearances – a process that of course commonly results in local rise in ground water levels. In zone VIII greatly diminished frequencies in eastern and southeastern England may well reflect intensive cultivation and drainage.

Tilia spp. (linden, lime), figure 8

Since the pollen grains of the two British species of lime tree, *Tilia cordata* and *T. platyphyllos*, are not separately identified in any but the most recent pollen analyses it is practicable now only to consider the limes as a genus.

There is little evidence for presence of *Tilia* in the British Isles in zones IV and V: pollen is recorded at few sites and always in very low concentration. In zone VI, however, it is established in considerable amount south of the Wash–Severn line and in northeastern England: elsewhere the occurrences are widely scattered and still of pollen in such low concentration that distant wind carriage seems their source. This restricted zone VI rise is generally concentrated in the latest part of the zone, heralding the dramatic expansion throughout England and Wales in the ensuing Atlantic period (zone VII a). It is to be noted that this expansion falls within the Hypsithermal Interval, in accord with the thermophilous character of the genus, and moreover that it has achieved its expansion against the competition of established oak–elm woodland. This is in contrast with the genera already considered – *Betula*, *Pinus*, *Corylus*, *Quercus*, *Ulmus* and *Alnus* – for which there is evidence of wide early presence through the country before their phase of establishment and consolidation. The evidence of such natural European woodlands as remain suggests that the two species of *Tilia* can have co-dominance with the oaks,

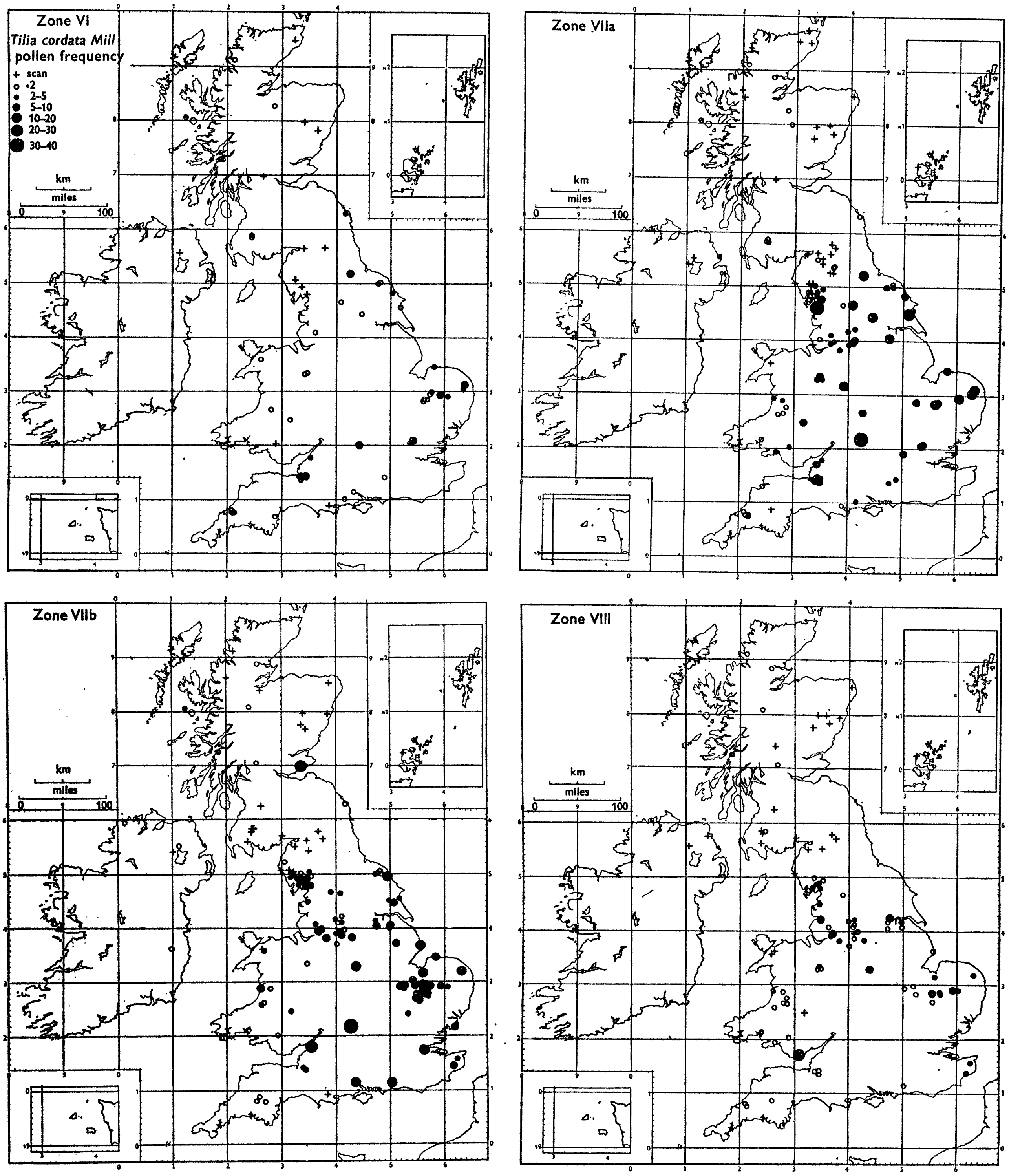

FIGURE 8. *Tilia* spp. Spot maps of the lindens (*T. cordata*, *T. platyphyllos*, and hybrids) for zones VI, VIIa, VIIb and VIII (*T. cordata* greatly preponderating) (see also figure 12).

and if we recall the strong under-representation of the entomophilous lime by its ill-dispersed pollen, it seems likely that it was a numerous component of the undisturbed mixed oak forests of zones VII a and VII b – indeed we may share Iversen's view that in Denmark '*Tilia* and not *Quercus* was the dominating tree in the climax forest of the Post-glacial warmth-period'. In zone VII b the range and frequency of *Tilia* pollen are unaltered, but in VIII, while the range is similar, sites of substantial abundance have become scarce. It seems likely that the value of the tree for leaf-fodder and bast fibre, as for easily worked timber, has induced strongly selective felling and suppression of it. There is no effective evidence to suggest that limes were ever native in Ireland or in Scotland except perhaps in Galloway.† It is plausible to suggest that the late westward migration of lime was interrupted by the Irish Sea, near its present height by the end of zone VI, but the absence from Scotland suggests also a natural thermal limit.

It is striking how closely the northern limit in zones VI–VIII appears to correspond with that of *Tilia cordata* at the present day (figure 12). Identification of fruits and flowers proves *T. platyphyllos* to have grown in England in the middle Flandrian in accord with the results of recent palynology, which shows that while the summer lime commonly occurred with *T. cordata*, it was in much lower frequency. In accord also with the higher thermal requirements of *T. platyphyllos* its records seem to be more sharply restricted to the warmest part of the Hypsithermal and occur most often in central and eastern England. The two species appear in the past, as in present-day woods, to have been accompanied by the hybrid between them, *Tilia* x *europaea*.

Fagus sylvatica (beech), figure 9

Although *Fagus sylvatica* is a dominant of the deciduous forest climax over large parts of continental Europe, it seems, as a natural dominant forest tree, to reach its present western and northern limits within the British Isles. In the Flandrian, as in preceding interglacials, the beech is strongly terminocratic. Its pollen frequency certainly under-represents the tree's abundance, so that the low and sparse pollen counts in zone VII a may still reflect local stands of the tree. In zone VII b we have numerous Neolithic and Bronze Age macroscopic records from south of the Wash–Brecon line together with pollen frequencies throughout England, Wales and Scotland that are difficult to appraise. The substantial spread of the beech certainly took place in zone VIII, particularly south of the Wash–Brecon line, but it seems probable that while natural beech woods were centred in this area, they also established themselves locally much further north. There seems good reason to suppose that the great expansion in *Fagus* pollen frequency during the Sub-Atlantic period was due, not to the increased climatic 'oceanicity' but to the manner in which the beech massively invaded those areas of former oak forest cleared by man and subsequently released for recolonization. This is expecially true of the chalk and other limestone hill country, and it is paralleled by similar behaviour of the tree (as also the spruce) on the west European mainland.

Carpinus betulus (hornbeam), figure 10

Like the beech, the hornbeam has behaved terminocratically in interglacials and in the Flandrian its history is closely similar to that of the beech except that the evidence is a good deal sparser with pollen frequencies much lower. Again the dated macroscopic remains from the Neolithic onwards and higher pollen frequencies indicate local hornbeam woods south of the

† The high value mapped in zone VII b for Fife has a special explanation.

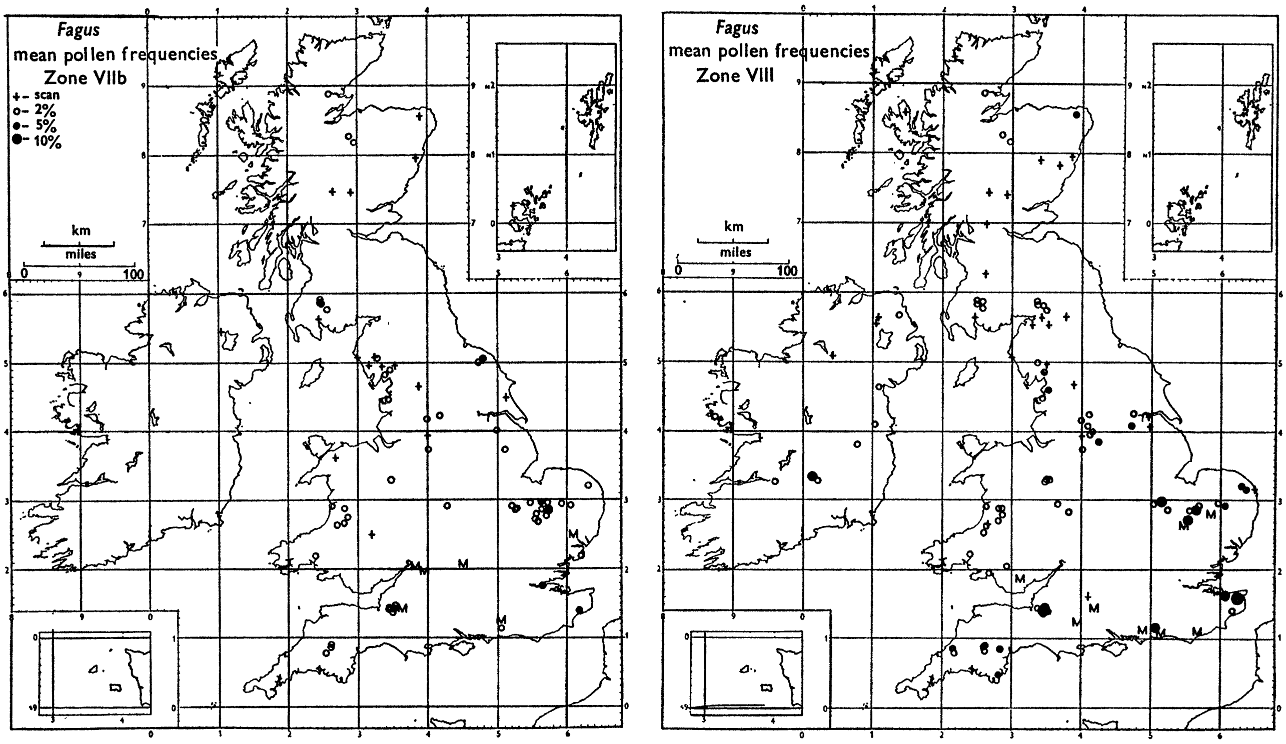

FIGURE 9. *Fagus sylvatica*. Spot maps for beech in zones VIIb and VIII. Macroscopic identifications (wood, charcoal) shown by M.

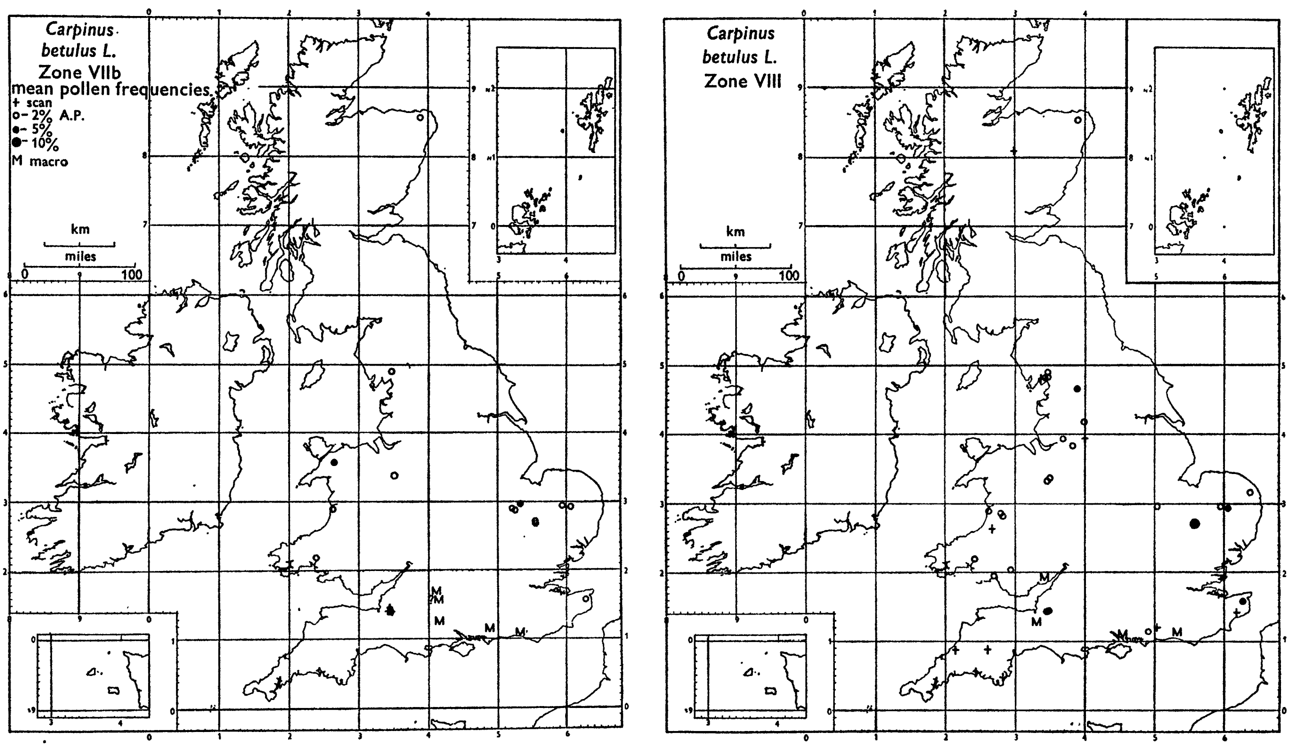

FIGURE 10. *Carpinus betulus* L. Spot maps for hornbeam in zones VIIb and VIII. M, macroscopic identifications.

Wash–Brecon line, and individual pollen diagrams reflect a similar response to the anthropogenic factor in zone VIII. There is little to indicate Flandrian hornbeam woods outside the area where they still seem to occur naturally, but it cannot be excluded that low pollen concentrations as far north as Lancashire and North Wales might have been due to local stands of the tree.

As with *Fagus*, it seems likely that the progress of the interglacial cycle at a late stage provides the hornbeam with a combination of both climatic conditions and the climatic soil type that it needs to achieve dominance or co-dominance with oak and beech. In the preceding Ipswichian interglacial these factors alone were effective, but in the Flandrian in Britain and the western European mainland the hornbeam's expansion was powerfully aided by forest clearance and subsequent abandonment.

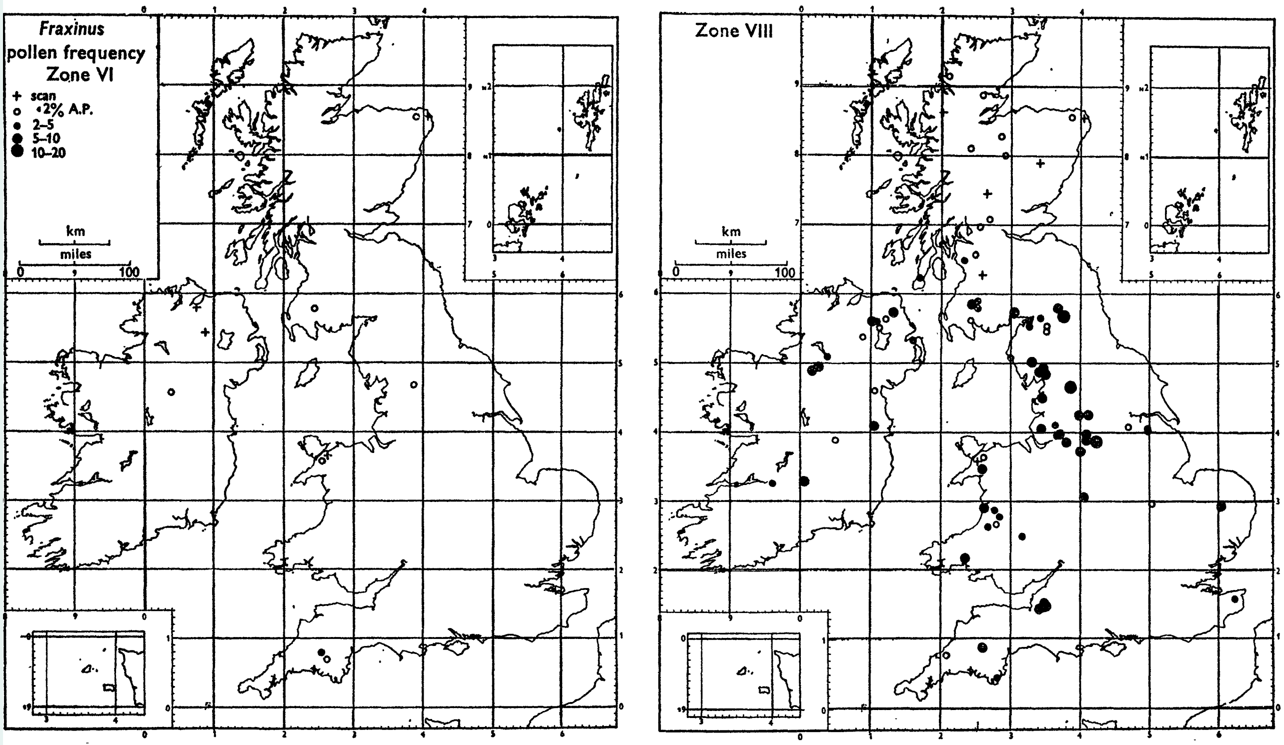

FIGURE 11. *Fraxinus excelsior* L. Spot maps for ash in zones VI and VIII.

Fraxinus excelsior (ash), figure 11

The ash has a continuous fossil record in the British Isles, increasing through the Flandrian in frequency from zone V to the present day. Its presence is attested by wood identifications from numerous archaeological sites from the Mesolithic onwards as well as from fen-wood peats, and the pollen record shows that whilst it was apparently present, though thinly, all through the British Isles in zone V, it increased in pollen frequency relative to other trees in each succeeding zone. The most dramatic increase, noted equally on the western European mainland, occurred at the opening of zone VII b and it has been convincingly attributed to response of the ash to the forest clearances then begun by Neolithic man. It is noteworthy that along with *Betula*, *Fagus* and *Carpinus* it also showed increased expansion in zone VIII in response to the more extensive forest clearances of Iron Age, Roman and later agriculturalists. Though evidently present continuously throughout the British Isles save perhaps the extreme north, it has also consistently displayed its greatest abundance in the western half of northern England, and to a less degree west Wales, Somerset and parts of Ireland.

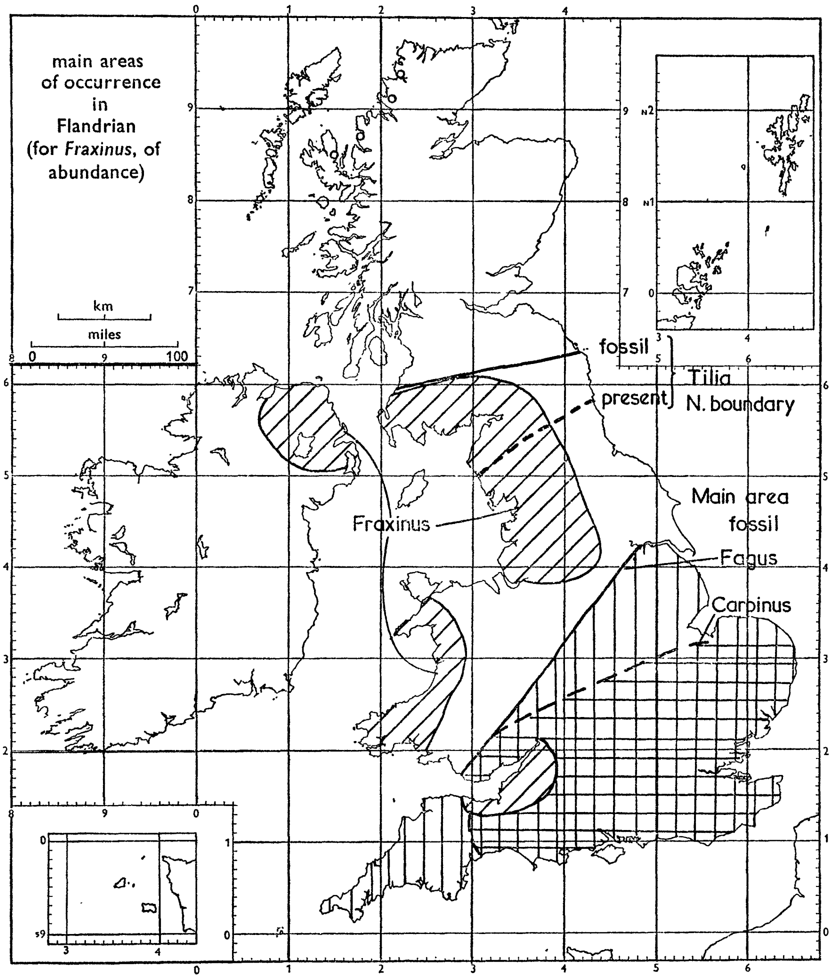

FIGURE 12. Main areas of beech, hornbeam and ash at their periods of greatest abundance in the Flandrian with the approximate northern limit of natural linden growth at present and during maximum Flandrian extension. The limes are strongly thermophilous and mediocratic, the beech and hornbeam telocratic, and the ash specially responsive to forest thinning and clearance.

The Flandrian history of the ash indicates a progressive build-up towards the present day when pure ash woods occur on the thin soils over older limestones of Derbyshire and the Mendip. This ash dominated woodland, not elsewhere known in Europe, thus seems unlikely to have been a natural climatic climax but to have had an anthropogenous origin, a conclusion to which the most authoritative modern ecological studies have also pointed Man played little part in modifying the forests of earlier interglacial periods and there is so far no trace in their records of abundant *Fraxinus* save in local fen woods.

Although thermophilous in comparison with elm and oak, the ash is evidently less demanding than the limes, beech and hornbeam, having not only a wider British range northwards than these genera but also with its area of highest abundance further north (figure 12). It is of course much the most Atlantic genus of the four

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Conclusions

Investigation of the Flandrian history of British woodland trees, especially seen against the background of their history in previous interglacial periods, casts helpful light upon the character and status of our chief native forest communities.

It is confusing that the time of human destruction of natural forest cover, roughly the last 5000 years, should also have embraced the decline of temperature since the thermal maximum and the increased oceanicity of climate of the Sub-Atlantic. None the less we may safely conjecture from the evidence already outlined that the natural recent forest climax over most of the British Isles was mixed oak woodland with elm, and in England and Wales one or both of the lindens. To the north of this in the Scottish highlands was the belt of natural pine forest, representing, as Tansley said, the westwards extension of the boreal coniferous forest zone. It is possible that in the extreme northeast birch was the climatic dominant. In southern, and especially southeastern England, it seems probable that beech and hornbeam were naturally dominant or co-dominant upon suitable soils.

At this stage two major considerations must engage us. The first is that a polyclimax rather than monoclimax situation prevailed throughout the country, in which local conditions of altitude, aspect, drainage and geology could determine variation from the broad climatic climax: thus alder was distributed in mosaic fashion through the undrained woodlands, possibly associated marginally with ash, and likewise beech and ash favoured limestone soils, and pine and birch altitudinal pre-climax sites, acid bogs and sandy or gravel soils. The second consideration is that although the climatic sequence of the interglacial cycle broadly controlled the nature of the climax forest formations, the progress of the 'clisere' was at a different rate on different soils. Thus on the igneous rocks of the Scottish highlands the progress of soil acidification and podzolization was much quicker than on the calcareous sedimentaries of southern England: correspondingly highland Scotland would have reached the telocratic phase of the interglacial cycle soonest, thus emphasizing the primary latitudinal gradient between the two regions.

In any attempt to equate British forest communities with those of mainland Europe it is evident that we have to view both categories as the products of successive cycles of Pleistocene climatic change. In each glacial episode forests were destroyed wholesale and their elements dispersed, and following each such episode there was progressive reinvasion from regions and localities of survival. In different interglacials the successfully reinvading trees may have differed and since the Tertiary there has certainly been progressive loss of species and of genetic range, so that for instance spruce and fir now no longer constitute part of our native woodland as they did in earlier interglacials. All the same, though depauperate in species, the integrative power of the remaining elements still constitutes climax deciduous woodland recognizably similar to that of the European mainland.

I have deliberately refrained from consideration of routes of re-entry of the different genera to this country after the last glacial period, or of the influence on their range of their respective powers of migration, although the natural absence of the lindens, beech and hornbeam from Ireland may be especially concerned with these factors. In attempting to elucidate the origin of woodlands it has seemed evident that the polyclimax interpretation accords perfectly with the wide early range (in low abundance) of all the genera, while allowing those widespread and dramatic increases of abundance that are consequent on large climatic shifts.

It will have become apparent that the effect of 5000 years of unique human destructiveness have removed most of the green forest mantle of these islands and that they have induced great changes in those examples of woodland that survive. In particular, trees generally characteristic of seral stages and secondary successions have enormously increased, above all the birches, and we have indicated that this effect appears also to have called into being our native ash woods, as well as having facilitated expansion of beech and hornbeam, trees that, in contrast with the ash, might very well have achieved local dominance even in the absence of man's

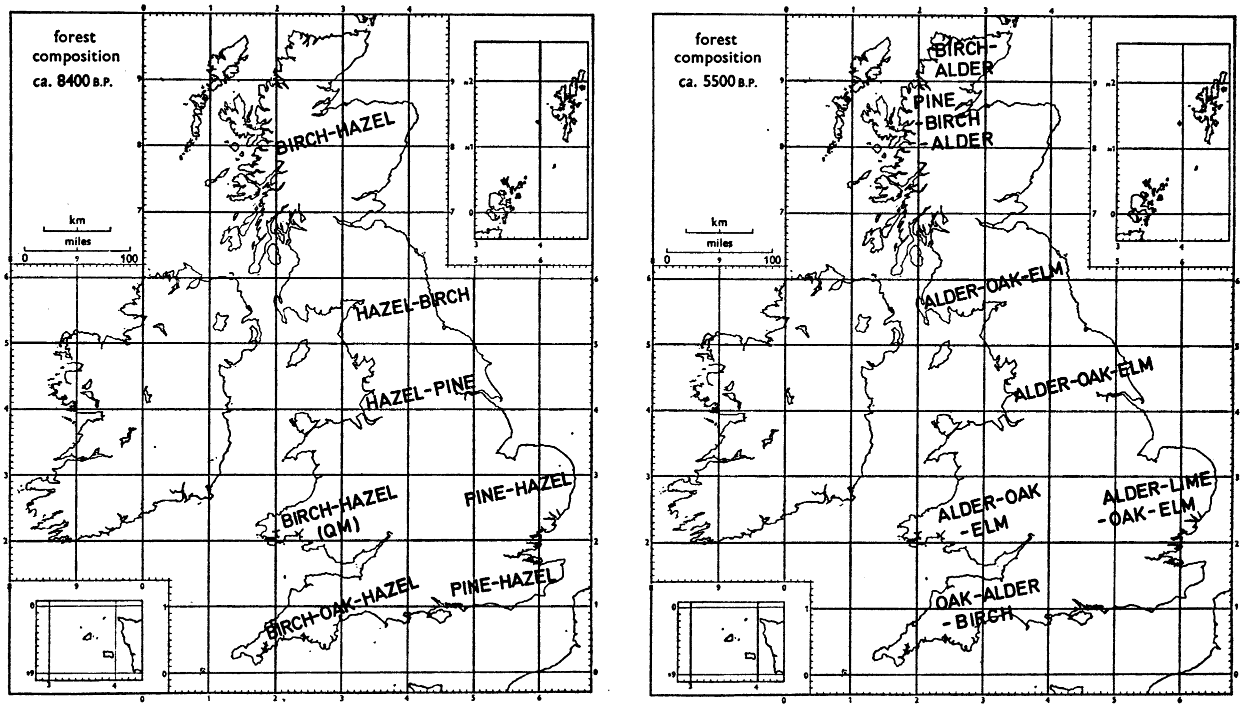

FIGURE 13. The natural forest communities of Great Britain indicated by pollen analysis for the time of the opening early-temperate substage of the Flandrian interglacial (*ca.* 8400 years B.P.) and for the thermal maximum just before Neolithic forest clearing (*ca.* 5500 years B.P.).

activities. It is apparent also that selective felling played a very important role from the early Neolithic onwards, in modifying forest composition (as particularly evident for the elm and the lindens) and it seems that coppicing had just as ancient an origin.

The Flandrian history of our trees provokes a further conclusion: it is the strong indication from the Boreal records that in the absence of mixed oak forest, pine could dominate virtually the whole of England and Wales, whatever the parent rock formation. Evidently as its own competition had suppressed birch and hazel, so it gave way to the spread of oak and elm. Within the closed deciduous forest of *Quercus* and *Ulmus*, *Corylus* was forced into a subsidiary role: only the lindens had the competitive power to enter and expand to share dominance within the undisturbed climax. Only locally and after disturbance were *Fagus* and *Carpinus* apparently able to do this.

Finally, it is worth drawing attention to the fact that the latitudinal and regional differentiation of our recent natural woodlands as now outlined follows a similar parallel (but not identical) spatial differentiation throughout the Flandrian. The two sketch-maps (figure 13) show that equally in the early Boreal and at the close of the Atlantic period the woodlands of Great

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Britain exhibited, just as now, the Scottish highlands on the one hand, and southeastern England on the other differentiated from the main central area. No doubt both climatic and soil differences have contributed to maintain this strong parallel development.

Discussion

J. L. Harley (*Department of Forestry, Oxford*)

I would like to ask Professor Godwin whether a comparative study of the variation in the subfossils of *Pinus* from northern Scotland and from the south of England gives any indication that they may have separate origin. Do they show any differences in width of variation in such characters as cone type, bark, needle length that are common in *P. sylvestris*?

Sir Harry Godwin

The speaker said that he had examined various exposures of buried pine forests of different ages in the south and east of England, with a view to comparing their cone, needle and bark qualities with those of the natural Scottish populations of pine. He had not found any conclusive evidence. Nevertheless it was to be hoped that opportunities for the collection and examination of subfossil pine of known provenances should be made as opportunity might offer.

J. Boss (*Medical School, University Walk, Bristol BS*8 1*TD*)

If the lime is associated with the warmest period, why is it now so characteristic of regions of central Europe with hard winters?

Sir Harry Godwin

The speaker said that there was no evidence that the Flandrian range of *Tilia* had been restricted by winter cold and it might well have been response to the high summer temperatures, also characteristic of central Europe, that determined its expansion in the Middle Flandrian.

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