



This is a peer-reviewed, post-print (final draft post-refereeing) version of the following published document and is licensed under Creative Commons: Attribution-Noncommercial-No Derivative Works 4.0 license:

Webb, Julia C ORCID logoORCID: <https://orcid.org/0000-0002-1652-965X> and Goodenough, Anne E ORCID logoORCID: <https://orcid.org/0000-0002-7662-6670> (2018) Questioning the reliability of “ancient” woodland indicators: Resilience to interruptions and persistence following deforestation. *Ecological Indicators*, 84. pp. 354-363. doi:10.1016/j.ecolind.2017.09.010

Official URL: <http://www.sciencedirect.com/science/article/pii/S1470160X17305782>

DOI: <http://dx.doi.org/10.1016/j.ecolind.2017.09.010>

EPrint URI: <https://eprints.glos.ac.uk/id/eprint/4943>

Disclaimer

The University of Gloucestershire has obtained warranties from all depositors as to their title in the material deposited and as to their right to deposit such material.

The University of Gloucestershire makes no representation or warranties of commercial utility, title, or fitness for a particular purpose or any other warranty, express or implied in respect of any material deposited.

The University of Gloucestershire makes no representation that the use of the materials will not infringe any patent, copyright, trademark or other property or proprietary rights.

The University of Gloucestershire accepts no liability for any infringement of intellectual property rights in any material deposited but will remove such material from public view pending investigation in the event of an allegation of any such infringement.

PLEASE SCROLL DOWN FOR TEXT.

Questioning the reliability of “ancient” woodland indicators: Resilience to interruptions and persistence following deforestation

Julia C. Webb* and Anne E. Goodenough

Natural and Social Sciences, University of Gloucestershire, UK

* Corresponding author:

Francis Close Hall, University of Gloucestershire, Swindon Road, Cheltenham, Gloucestershire, GL50 4AZ, UK

Abstract

Indicator species can provide invaluable insights into environmental conditions but robust empirical testing of their effectiveness is essential. Ancient woodland indicators (AWIs) are plant species considered indicative of sites that have been continuously wooded for a long period by virtue of poor dispersal ability and intolerance of non-woodland habitats. Many countries now utilise AWI species lists to classify ancient woodlands. Here we use a metastudy approach to test resilience of AWIs to interruptions and persistence following deforestation – and thus the robustness of using AWI lists – using a novel approach. We compare current AWI assemblage with woodland history based on pollen evidence at nine sites across the UK with a robustly-dated and spatially-precise palynological profile. Sites were split into: (1) proven continuous woodland; (2) previously interrupted woodland; and (3) previously but not currently wooded. Vegetation history was >1000 years at most sites. Assessment of ancientness using AWIs agreed with palynologically-proven ancient woodland at two sites, including a species-poor woodland of previously-uncertain age. However, four interrupted woodland sites and three clear-felled sites supported extensive AWI floristic communities. This suggests AWIs are resilient to interruptions, possibly by remaining in the seed bank longer than expected, and persistent following deforestation. Persistence might be due

to other species (e.g. heathland plants) acting as pseudo-canopy or because some AWIs are more tolerant of non-woodland locations than previously thought. We conclude that use of floristic AWIs alone in defining ancient woodland should be reviewed, especially where status links to planning policy and conservation prioritisation. We suggest species on AWI lists be reviewed under expert and local guidance and a system of weighting species based on their strict or strong affinity solely with ancient woodland be developed. The use of multi-taxa indicators is recommended to allow stakeholders globally to make informed decisions about ancient woodland status.

Keywords

Ancient woodland, old-growth forest, indicator species, vascular plants, conservation.

1. Introduction

Indicator species are organisms whose presence, prevalence or abundance is indicative of environmental conditions within a particular ecosystem. Use of indicator species is especially helpful when they allow inferences to be made about parameters that are difficult or expensive to measure directly (Landres et al. 1988; and McGeoch 1998). While indicator systems can be based on individual species (e.g. using the abundance of a moss, *Hylocomium splendens*, to indicate heavy metal pollution in Alaska: Hasselbach et al., 2005), any system that uses one line of evidence is prone to atypical results. Accordingly, community-based approaches based on multiple species are usually more robust.

In woodlands, species communities can be useful in determining whether a site has been continuously wooded over a pre-determined time period and thus meets the threshold for being considered “ancient” (European terminology) or “old-growth” (American terminology). Ancient woodland is often regarded as having a higher conservation priority, and being worthy of greater protection, than recent woodland (Goldberg et al., 2007). This is because ancient woodlands support highly-specialized or disturbance-sensitive species that are frequently absent from recent woodlands (Peterken and Game, 1984; Rotherham, 2011). Many such species are rare or declining (Kimberley et al., 2013) and ancient woodland itself is often threatened and fragmented (Spencer and Kirby, 1992; Palo et al., 2013; Swallow and Goodenough, 2017). Ancient woodland is thus protected in most countries in planning legislation and land use policies (e.g. National Policy Planning Framework in UK).

Because of the value placed upon ancient woodland, and the way that it is imbedded within planning and conservation practice, it is necessary for ecologists to have an accepted demarcation between ancient and recent sites. The definition of what constitutes “ancient” or “old growth” woodland varies geographically based on climax community type and natural fire regime. In the Netherlands and coastal Canada, ancient woodlands are regarded as <1850AD (Grasholf-Bokham, 1997; Wells et al., 1998) whereas ~1770AD is used in Denmark and ~1750AD in Germany (Petersen, 1994 and Zacharias, 1994, respectively). In the UK, ancient woodlands are areas greater than 2 ha (Goldberg et al., 2007) that have been wooded continuously and relatively undisturbed since 1600AD in England/Wales and 1750AD in Scotland – i.e. >400 calendar years before present (cal. BP) (Peterken, 1981; Rackham, 2003).

Even where accepted definitions of ancient woodland exist, there is often limited evidence upon which to draw when considering the ancientness status of a specific site (Rackham, 2003). Cartographic information can be useful for the last 150-200 years (occasionally more: good map coverage exists from the late 1700s for Essex, UK: Chapman and André, 1777). Estate maps can be helpful but coverage is patchy (Rotherham, 2011). Historical records can sometimes push documentary evidence back further but, even where records exist, information is often vague and locations can be hard to pinpoint accurately (Rackham, 2003). Examining the age of trees, either via dendrochronology (O’Sullivan and Kelly, 2006) or by measuring diameter at breast height (e.g. Rotherham et al., 2008), can be important but these methods are not without problem. Firstly, not all ancient woods support veteran trees due to frequent turnover due to natural disturbance and regeneration, harvesting management, or because the local conditions do not favour development of over-mature specimens, possibly due to shallow earth or exposure. Secondly, the presence of veteran trees does not axiomatically mean woodland is ancient as it could substantially post-date the veterans.

1.1 Ancient Woodland Indicators

In 1898, Buchanan White first noted that old pine forests of Scotland supported plant species that were much less common in recent or disturbed woods (e.g. Twinflower *Linnaea borealis*, Creeping Lady's-tresses *Goodyera repens* and One-flowered Wintergreen *Moneses uniflora*). More systematic study some 76 years later suggested this was part of a more widespread trend with ~30% of woodland plant species seeming to be consistently found at ancient woodland sites (Peterken, 1974). This led to a list of Ancient Woodland Species (AWS) being devised for the UK, with subsequent lists being developed for other countries including in the USA (e.g. Marcot et al., 1998) and countries in mainland Europe (e.g. Honnay et al., 1998; Schmidt et al., 2014; Wulf, 1997). Although those devising the different lists variously used expert opinion, ad-hoc field data, or systematic surveys (with or without statistical testing) the aim remained consistent, viz. identifying species that could be used as Ancient Woodland Indicators (AWIs).

There is an elegant simplicity about using the very species supported by ancient woodland to indicate ancient status (or otherwise) of woodlands. Given the weaknesses inherent in single-species indicator systems, inferences on ancientness are not based on presence of individual species but rather on the presence of multiple species using a community-based approach (Hermy et al., 1999; Kirby et al., 1998; Spencer, 1990). Because of the effects of geographic area, regional species lists have since been developed in many countries (e.g. Glaves et al., 2009). AWIs generally have similar life-history traits: they are disturbance-sensitive (Hermy et al., 1999; Honney et al., 2002), they are slow to colonise and have poor dispersal abilities (Nilsson et al., 2001; Nordén and Appelqvist, 2001; Peterken, 1974), and they are intolerant of non-woodland conditions as they need shelter and consistent humidity (Barkham, 1992). In terms of physical characteristics, many AWIs are short perennial species (Kimberly et al., 2013) and some have niches based on dead wood or other dead organic matter (Hodge and Peterken, 1998). Soil or other physical conditions might also need to be well established; for example, De Keersmaeker (2004) has found the soil on land previously used for farmland is too immature to accommodate AWIs even when it becomes wooded.

Use of AWIs is widespread both in terms of woodland ecology research (e.g. Kimberley et al. 2013; Stefańska-Krzaczek et al. 2016) and practical conservation (e.g. Goldberg et al., 2007; Kirby and Goldberg, 2002). For this to be robust, it is vital that the AWI approach itself is robust. The initial compilation of AWI lists has largely been based on species presence within “known” ancient woodland but this rationale is somewhat circular (Spencer, 1990), especially if non-ancient (and indeed non-woodland) sites are not included for comparison purposes. Moreover, it is often very difficult for woodlands to be definitively known to be ancient and continuously wooded for 400 Cal. BP because of the above-mentioned lack of historical and cartographic evidence. This means that some sites typically regarded as ancient, and used to inform AWI lists, might actually be more recent or have a history of interruptions (Day, 1993).

1.2 Use of palynology in woodland ecosystems

The use of fossilised biological remains to reconstruct past environments is well established. This can involve assessing palynological evidence (pollen grains and spores) to identify environmental change (e.g. Tzedakis, 1997) and human influence (e.g. Bryant and Holloway, 1983). Interpreting palynological data requires an awareness of the ecological process that underpin pollen dispersal and preservation. Pollen grains, particularly those that are anemophilous (wind-dispersed), can travel long distances (Fægri and Iversen, 1964), which means that the pollen within natural successional layering of sediment at a site will be influenced not only by immediate vegetation but

also the *regional* pollen signal; this is especially true at exposed sites such as peat bogs (e.g. McCarroll et al., 2015). In forest hollows or wet ditches, however, the palynological profile is influenced less by pollen morphology (e.g. Xu *et al.*, 2016) and more by the sheltered nature of the area. Only very local vegetation tends to be represented in the profile as the surrounding canopy will prevent pollen dispersing from the site or being introduced from elsewhere via air currents. Although pollen rain from external sources could constitute a very minor part of a palynological profile, pollen fossilised within a peaty woodland hollow largely records *local* vegetation history.

To date, palynological investigation within woodlands has focused upon reconstruction of plant communities to: (1) infer species history (Baker et al., 1978; Bradshaw, 1981); (2) understand the effect of humans on local landscapes (Oldfield et al., 2003); (3) inform restoration management (Brown, 2010; Grant and Edwards, 2008); or (4) explain apparent disconnects between current vegetation and soil type (Dimpleby and Gill, 1955). Palynological profiling has seemingly never been used at a multi-site scale to provide empirical data against which AWIs can be compared. The only study to attempt something similar is Ohlson et al. (1997), which compared epiphytic lichen and saproxylic fungi indicative of old-growth spruce forests with paleoecological records. Intriguingly, this found no relationship between the occurrence of 33 indicator species and the actual time since disturbance (300–2000 years). Rolstad *et al.*, (2002) advocated undertaking a similar study for flora and highlighted comparing AWI communities to known (rather than inferred or supposed) vegetation history as being a research priority. Here, we use a metastudy approach to compare woodland history based on palynological evidence with current AWI species assemblage for sites across the UK to establish the resilience of AWI species to interruptions and their persistence following deforestation.

2. Methods

To inform the metastudy, sites were selected based on: (1) availability of a published, robustly-dated, palynological profile that was spatially precise and thus gave a record of local woodland continuity without being unduly influenced by the regional pollen signal and (2) presence of detailed contemporary vegetation data collected through modern primary surveys. Only sites where data were derived from experienced fieldworkers were included to reduce the chances of misidentifications; data also needed to be reasonably comprehensive to minimise false absences. Current woodland vegetation was ascertained from a variety of sources, including published literature and consultancy research reports, as well as records held by county records centres, county recorders, reserve managers or wardens, or regulatory bodies such as Natural England.

In total, nine main sites fulfilled the above criteria. These were widespread geographically (Figure 1). Two island sites were represented: Shetland in Scotland and Skomer in Wales. In all cases, the pollen cores were taken from within the woodland (or former woodland) boundaries. Coring sites were damp hollows or ditches or, in two cases (Garbutt Wood and Gunnister), a small closed-system lake fully surrounded by woodland. All cores were complemented by radiocarbon dates, which was essential in order to compare woodland age to established thresholds for ancient woodland and to date any interruptions to woodland continuity. In some cases, radiocarbon dates were cross-calibrated with known events in vegetative history such as planting of *Pinus* (e.g. Derrycunihy Wood in Southwest Ireland; Mitchell, 1988) or elm decline (e.g. Sydlings Copse in Oxfordshire: Day, 1993). Two additional sites, Winding Stonard Wood in Hampshire and Oxborough Wood in Norfolk, were also evaluated but conclusions here were more limited because the cores were not dated (Figure 1). Details of the sources of palynological information for each study site are given in Table 1.

The current vegetation at each site was compared to the master AWI list compiled by Glaves (2009), which brought together lists in Rackham (2003) and 37 regional lists, as well as additional species listed by Peterken (1974), or that occurred on the Northern Island or Durham AWI lists (Durham County Council, 2008; Woodland Trust, 2007). This master list included trees, shrubs, forbs, graminoids and non-flowering species (bryophytes and ferns). In addition, vegetation was specifically compared to the nearest local AWI list (for the relevant county if possible; if this did not exist the relevant regional list was used) and the strict/strong indicators listed by Rackham (2003). We recognise that using national lists is not ideal, but local lists were unequal in size and so it was impossible to directly compare sites in different regions without using national lists. Glaves (2009) also notes the robustness of local lists is questionable due to variable attitudes and awareness of those compiling the lists. By using both national and local lists, we avoided relying solely on local lists but also gained the benefit of local knowledge where appropriate. Where possible, we noted temporal fluctuations in specific AWIs within the palynology record but this was only feasible for species that could be identified to species level from pollen remains: *Hyacinthoides non-scripta* (bluebell), *Anemone nemorosa* (wood anemone), and *Mercurialis* (dogs mercury) (Brown 2010; Day, 1993).

There has been discussion in the literature (Glaves, 2009; Honnay, 1998) on the threshold criteria for the minimum number of plant species present to denote an area as ancient woodland. Glaves (2009) notes that the recommendation in parts of South Wales is areas with ≥ 12 AWIs are classified as ancient, but in Bedfordshire this drops to ≥ 5 AWIs. Honnay et al., (1998) showed 25-27 plant species were needed to discriminate between ancient and short continuity cover. Any threshold values will axiomatically link to woodland size and thus survey area has been noted in Table 1.

The sites studied in this paper fall into three main groups: (1) sites with a palynologically-proven continuous history of woodland (Figure 2); (2) sites that are currently wooded but that have also had interruptions to their woodland coverage as revealed by changes in the species represented in the pollen core (Figure 2); and (3) sites that are not currently wooded, and in some cases have not been for some time according to pollen cores, but that currently support an AWI species community (Figure 2). These scenarios will be considered in turn to critically examine any difference in AWIs relative to woodland continuity and thus the resilience of AWIs to interruptions and their persistence following deforestation. The number of AWI species found at each site in different vegetation groups is given in Table 2. Full details of the exact species found at each site is given in the supplementary material.

3. Results and Discussion

3.1 Palynologically-proven continuous ancient woodland

Derrycunihy Wood in Southwest Ireland lies in the Killarney valley and comprises part of the greatest extent of ancient woodland in Ireland. The current woodland is dominated by *Quercus petraea* with frequent *Betula pubescens* and *Sorbus aucuparia* and an open understory of *Ilex aquifolium* (Kelly, 1981). The woodland also has a rich Atlantic bryophyte flora (Ratcliffe 1968). The pollen history, based on core taken from a wet hollow within the wood by Mitchell (1988), suggests that the site was characterized by stable closed canopy woodland dominated by *Betula*, *Pinus* and *Quercus* between around 4,850 Cal. BP (radiocarbon date) and 2,400 Cal. BP (interpolated date). Around 2,400 Cal. BP, the canopy started to open up considerably with increasing *Plantago*, suggesting disturbed ground, and also *Pteridium*. There was also increased evidence of charcoal, suggesting fire clearance, at this time. The canopy started to close once more around 1,290 Cal. BP but the woodland seems to have remained more open than previously for some considerable time before becoming denser towards the present day. There is continued evidence of fire throughout this time as well as, latterly, a decrease in floristic diversity that Mitchell (1988) ascribes to intensive sheep grazing since the 1900s. Palynological evidence, therefore, suggests that this site has been continually wooded for at least 5,000 years albeit with a long history of human influence. Contemporary vegetation records show that the site has a good AWI community with 28 AWIs in total of which 7 are locally-listed. Although there are AWIs in all vegetative groups, the importance of the non-flowering species is striking with 11 species of AWI bryophyte or fern. Two strong AWIs are present: *Oxalis acetosella* and *Lysimachia nemorum*. Derrycunihy thus exemplifies the range and diversity of AWIs present at a site with continuous woodland coverage, which has been proven objectively rather than simply assumed or inferred from documents, and acts as a baseline against which other sites may be compared.

While Derrycunihy is reasonably species-rich, some woodland sites are more homogeneous and thus relatively species-poor. Inferring habitat age based on AWI species could be problematic at such sites for two reasons. The first issue is that ancient woodland sites often have a greater floristic diversity than more recent sites (Dzwonko, 1993; Jacquemyn et al 2001) and so potential ancient sites could be missed if initial assessment is simply based on plant richness without simultaneous consideration of other evidence. The second issue, somewhat paradoxically, relates to one of the normal strengths of AWI: that is a community-based approach. As noted above, community-based indicator systems are usually more robust than single-species indicators, however, their Achilles heel is that they can be hard to apply if the species community is itself impoverished. It is thus possible that, in some cases, there might be insufficient AWIs to reach the accepted thresholds for declaring a site to be ancient (Glaves, 2009; Honnay, 1998).

An example of a species-poor woodland is Wistman's Wood in Devon, a National Nature Reserve that is characterized by stunted *Quercus robur* and exposed granite boulders. There is very little ground flora but there is a diverse bryophyte assemblage (Proctor, 1962; Simmons, 1965). The site has typically been considered to be ancient based upon an assumption of woodland continuity (Coppins and Coppins, 2005) and its landscape context as a remnant patch. However, doubt was cast on the site's woodland age by Coppins and Coppins (2002), who studied the lichen species indicative of old growth woodlands using the Revised Index of Ecological Continuity (RIEC) system (Rose 1976, Rose and Coppins 2002). Wistman's Wood was given a REIC score of 10, which did not support old growth status (Coppins and Coppins, 2002). To provide a definitive answer, Bradshaw et al. (2015) took a pollen core from a pocket of humus accumulation amongst the boulders; this had a basal date of 1,200 Cal. BP. The pollen evidence suggests that between 1,200 and 900 Cal. BP the woodland was relatively diverse, being dominated by *Quercus* (as currently) but also with *Alnus*, *Betula*, *Corylus*, and *Fraxinus* represented. The presence of notable amounts of *Calluna* suggests that the woodland was quite open. The diversity of arboreal pollen decreased over time to 170 Cal. BP where the woodland became much more homogenous. Charcoal and *Plantago* were found throughout, suggesting human influence. Based on this palynology study, and despite times when the arboreal pollen concentration dipped to ~25%, the site appears to have been wooded continually for at least the last 1,200 years. This interpretation - that such dips were periods of more open woodland rather than such dips being woodland clearance - is strengthened by there being no other woodland in the immediate area, such that there would be little regional arboreal pollen signal. The site now contains 24 AWI species, including 6 non-flowering species and one strong AWI indicator: *O. acetosella*. This suggests that although lichen diversity in the woodland might be insufficient for the site to be deemed old growth, the plant AWI assemblage

would meet accepted criteria. This reinforces the value of using multiple taxonomic groups in ecological indicator frameworks, as well as providing a baseline with which other species-poor woodlands can be compared.

3.2 Interrupted woodland: AWI resilience

Undertaking palynological work is a powerful way of identifying and dating historical interruptions to woodland coverage. Such interruptions are characterised by changes in the species represented in the pollen core; in particular a sudden and substantial decrease in arboreal pollen and a simultaneous increase in Poaceae and/or Cyperaceae, as well as an increase in species characteristic of disturbance such as *Potentilla*.

Garbutt Wood in the Northeast of England is a Site of Special Scientific Interest (SSSI) and a Yorkshire Wildlife Trust nature reserve. It is dominated by *Quercus* and *Betula* with a *Pteridium* field layer. Palynological work has focused on cores from Goremire Lake, a water body approximately 150m wide and 300m long that is fully encircled by the woodland. The lake has a closed basin hydrological system, thereby minimizing the entry of pollen entry from wider catchment. Although some overland flow is possible, any effect is considered minor (Blackham et al., 1981; Oldfield et al. 2003), such that pollen recruited into lake sediment is primarily from direct lake catchment (i.e. Garbutt Wood). The site was first cored by Blackham et al. (1981). This study showed that, contrary to local belief, the site was unlikely to have been continually wooded but instead had a period of clearance characterized by a reduction in arboreal pollen and a simultaneous increase in non-arboreal pollen. However, this core was undated so the timing and duration of the interruption was unknown. To address this, analysis of a dated core (spanning approximately 3,500 years) was undertaken by Oldfield et al. (2003). This showed an interruption to woodland coverage between 2,200-1,400 Cal. BP. Before this, the site was characterized by closed canopy woodland dominated by *Alnus*, *Colylus*, *Betula*, *Fraxinus*, *Quercus*, *Salix* and *Ulmus*. During the interruption, total arboreal pollen decreased to ~10% and there was a corresponding peak in Poaceae, *Plantago* and *Pteridium*. Following this interruption, the woodland regenerated and has remained continuously wooded since (albeit with a long period of what seems to be more open woodland between 800 and 200 Cal. BP). Today, the site has an extremely rich AWI species assemblage, with 72 species in total distributed across all species groups. Three strong AWIs are present: *A. nemorosa*, *O. acetosella* and *L. nemorum*.

The comparison of palynology and current AWI floristic community at Garbutt Wood suggests that AWI species assemblages can be resilient to an historical interruption in woodland coverage, possibly because species remain in the seedbank during interruptions or are able to grow in non-wooded conditions during the interruption. However, in

the case of Garbutt Wood, the length of time between the interruption and the current day is substantial – around 1,400 years – such that AWIs could have recolonised in the intervening period. Analysis of sites with more recent interruptions, including Sydlings Copse in Oxfordshire, Piles Copse in Devon and Johnny Wood in Cumbria, would thus be useful.

Sydlings Copse is a SSSI managed by the Berkshire, Buckinghamshire and Oxfordshire Wildlife Trust. It is one of the most well-documented woodlands in the UK due to its location within the royal mediaeval forest of Stotover and Stowood. Written records and cartographic evidence suggest the site was wooded in 1660 AD (340 Cal. BP) when it was listed as part of a ~240ha wood (Day, 1993). Before this date, though, vegetation history is less certain, making this site a good candidate for palynological study. Extraction of a pollen core from a woodland ditch by Day (1993) produced a pollen sequence spanning approximately 9,500 years, but accurate dates were only possible in the upper section (earliest radiocarbon date = 3,820 Cal. BP). The very oldest deposits show, as expected, an initially herb-dominated community with increasing *Corylus* and *Pinus sylvestris*. By the first radiocarbon date of 3,820 Cal. BP and up until 1,800 Cal. BP, the profile shows evidence of woodland continuity with *Corylus*, *Tilia*, *Alnus* all dominant or co-dominant at different times, together with a presence of *Ulmus* and *Quercus*. This period was followed by an abrupt change between 1,800 and 1,000 Cal. BP when arboreal pollen was replaced almost completely by herbs and *Pteridium* with just a small amount of *Salix* (at maximum 20%) for a period of 800 years. This was followed by a period of woodland regeneration from 1,000 Cal. BP with continuous woodland present from this time to the present day. The contemporary woodland records show a plant community with a rich AWI species assemblage. In total, 75 AWIs are present, including 14 locally-listed and several strong indicators: *A. nemorosa*, *Campanula trachelium*, *Euphorbia amygdaloides*, *Hypericum hirsutum*, *O. acetosella*, *L. nemorum*, *Paris quadrifolia*, *Carex pallescens* (identified as a strict AWI by Rackham (2003)), *Carex remota*, *Luzula pilosa*, *Melica uniflora* and *Milium effusum*.

Palynological evidence from a different site, Piles Copse in Devon, points to there being an interruption to woodland continuity at a similar date to Sydlings Copse, but it in a very different type of woodland. Similar to Wistman's Wood (see above), Piles Copse has a species-poor community. Many of the trees are stunted and the ground flora is sparse, while the bryophyte community is both rich and abundant (Ratcliffe, 1968). Initial speculation as to the origins of the woodland (Simmons, 1965) highlights the fact the woodland is an isolated patch in an otherwise non-wooded landscape. Early palynological work in the 1990s took cores from flush bogs immediately adjacent to the site (Roberts and Gilbertson, 1994). This suggested that there had been a lengthy interruption to woodland within the last 2,500 years. However, as

the core was undated and taken from outside the woodland, conclusions remained rather non-specific. A second study (West, 1997) provided dated evidence from two cores within the woodland using radiocarbon analysis. This work suggested that <600 Cal. BP, there was mixed woodland characterized by *Quercus*, *Corylus*, *Betula* and *Ulnus*. At around 600 Cal. BP, the arboreal pollen decreased to a trace occurrence (<1% of the total pollen sum) with a simultaneous decrease in *Polypodium* suggesting complete woodland clearance. At the same time, there was sharp rise in Poaceae, Cyperaceae, and *Potentilla*. Sphagnum moss also disappeared at this point, suggesting drier conditions (McCarroll *et al.*, 2015). The hiatus in woodland spanned a period of 15cm (from a total 30cm) in the sediment record younger than 600 Cal. BP, with woodland regeneration only showing within the last 15cm of sediment accumulation. This suggests that the site could be borderline in terms of whether it is its actually ancient based on traditional criteria (making the very large assumption of sediment accumulation being temporally consistent and not affected by erosion, woodland regeneration would have started at 300 Cal. BP, whereas the ancient woodland threshold is 400 Cal. BP). Despite having a very species-poor community, the site currently supports 12 AWI species, including the strong indicator of *O. acetosella*. This is half the number found at Wistman's wood, a similar woodland in terms of location, structure, species richness, and species community but which has been wooded continually for the last ~1300 years rather than for the last ~300-500 years.

A site with an even more recent interruption, but high conservation value, is Johnny Wood in Cumbria, Northwest England. This is a SSSI, part of Borrowdale Woods Special Area of Conservation, and lies within the Lake District National Park. The site is covered by broadleaved woodland dominated by *Q. petrea* and is noted for its bryophyte community. Palynological investigation of a short core taken from a woodland hollow by Birks (1993) showed that the site supported mixed deciduous woodland prior to 140 Cal. BP (basal date unknown; 12cm of sediment accumulation <140 Cal. BP). This woodland was species-rich, with *Alnus*, *Betula*, *Corylus*, *Fraxinus*, and *Quercus* with low levels of *Salix*, *Taxus*, *Tilia*, and *Ulmus* and an understory of Poaceae and Polypodiaceae. Between around 140 and 100 Cal. BP, there is a clear interruption that has been interpreted as localized woodland clearance by Bradshaw *et al.* (2015) with a residual regional signal. This is characterized by a rapid decline in all arboreal pollen and a substantial increase in Poaceae, *Calluna* and *Potentilla*. Following this period, the woodland recovered but with a different composition to before the interruption, with *Alnus*, *Corylus* and *Fraxinus* all present in trace amounts but other species, including *Acer*, *Larix* and *Ilex*, appearing for the first time and *Sorbus* having a greater presence than before the clearance, albeit only marginally. The time of this interruption actually means that, by

conventional criteria, this site should not be regarded as ancient. The current AWI species community, however, is rich and diverse, with 46 species present including the strong indicators of *C. remota*, *L. pilosa*, *L. nemorum* and *O. acetosella*, indicating the ecological value of the site.

The concept of persistence in seed banks is supported by consideration of another site: Oxborough Wood in Norfolk. A 3m core was taken from a woodland hollow (Bradshaw, 1981) but was undated so interpretation is challenging. The site is currently a plantation: *Populus* was planted around 1930 and then clear felled in all but the wettest areas in 1953, at which time *Pinus* was planted. The site appears to have been continuously wooded from the time of the bottom of the core (313 cm) until 62 cm depth. Within this period, the woodland composition changed with shifts in the dominant species (*Betula* followed by *Pinus/Corylus*, and finally *Quercus*, *Alnus* and *Tilia*) but continuity remained. After this time, arboreal pollen decreased to ~15% of the total pollen sum, which Bradshaw (1981) interpreted as a period of clearance. At this time, Poaceae and Cyperaceae become dominant, with *Plantago*, Polypodiaceae and *Pteridium* as well as a background regional signal of *Corylus*, *Alnus* and *Quercus*. Based on documentary evidence, it is likely that the plantation was created sometime between 1797, when the site was not marked as woodland on a detailed map of the area, and 1845 when it was listed on a county audit as a plantation (Bradshaw, 1981). The current plantation woodland contains 13 AWI species, including two that are local indicators. Given the comparatively short amount of time (~200 years) between the likely timing of woodland planting (following a period of clearance) and the present day, it seems most likely the AWIs currently present at the site remained during the hiatus, either growing or in the seed bank, since recolonization of all 13 AWI species presently found within that time is unlikely.

3.3 Cleared woodland: AWI persistence

The above sites are examples of areas that are currently wooded but have had interruptions to woodland coverage and provide useful insights in AWI *resilience*. A somewhat different scenario is afforded sites that have been wooded in the past but that do not currently support woodland vegetation. Consideration of such sites allows insights into AWI *persistence* in non-wooded environments.

Hartlebury common, Worcestershire, is dominated by *Calluna vulgaris*, *Erica cinerea* and *Ulex gallii* with patches of *Pteridium*, grassy areas, and occasional *Betula* and *Quercus* seedlings and saplings. The site is a SSSI by virtue of being one of the most important areas of dry dwarf shrub heathland in central England. Analysis of a pollen core taken from a wet depression, however, suggests that the site used to be wooded (Brown, 1984). The pollen record shows that

between 9,710 and 2,610 Cal. BP, the site was dominated by *Pinus*, *Ulmus*, *Corylus*, and *Betula*, with some *Quercus* and *Alnus*. The dominance of *Pinus* and *Corylus* decreased in the latter part of this period. After around 2,610 Cal. BP, the vegetation changed: arboreal pollen decreased to ~15% and the previously-dominant *Pinus* and *Ulmus* were lost. Instead, Poaceae and Cyperaceae became dominant with *Erica* increasing within the pollen profile over time with lower levels of *Betula* and *Quercus* remaining. This suggests a change from woodland to a grassland/heathland matrix with scattered *Betula* and *Quercus*, much as per the present day. Despite the site not being wooded currently, and seemingly not wooded since 2,610 Cal. BP, it still supports 21 AWI species, the majority of which are non-woody.

Gunnister, on the main isle of Shetland, currently supports mixed grassland and wet heathland dominated by Cyperaceae, *Sphagnum* and *C. vulgaris*, with abundant Poaceae (especially *Nardus stricta*). As a whole, Shetland today is almost completely devoid of trees (Johansen, 1975; Scott and Palmer, 1987) although evidence of tree roots, woody debris and palynology suggest that the islands were once extensively wooded (Bennett et al., 1997; Birnie, 1984). Palynological analysis of Gunnister by Bennett et al. (1993) suggests that this particular site was wooded until around 2,685 Cal. BP. Before this time, arboreal pollen was abundant and diverse, initially (from 9,405 Cal. BP) comprising *Betula*, *Corylus* and *Pinus*, with *Ulmus*, *Quercus*, *Salix* and *Alnus* entering the pollen record between 9,405 and 2,685 Cal. BP. Since 2,685 Cal. BP, grassy heathland has predominated, with *Calluna* and Cyperaceae increasing over time and Poaceae occurring at a consistent ~20-25% of the total pollen sum. *Sphagnum* and Cyperaceae have increased, suggesting that the area has become wetter over time. Charcoal, which previously only occurred infrequently and at negligible levels, increased from 2,685 Cal. BP, suggesting burning and human disturbance after this date. Despite their currently being no trees at the site (or indeed regionally), and palynological evidence suggesting the area was last wooded over 2,500 years ago, the site still supports 20 AWI species. This is split approximately equally between forbs, grasses and non-flowering species.

The situation is similar, but even more dramatic, on another island: Skomer, off the Pembrokeshire coast in Southwest Wales. This currently has a maritime vegetation community, which comprises *Crithmum maritimum*, *Spergularia rupicola*, *Festuca rubra*, *Armeria maritima*, *Holcus lanatus*, and *Rumex acetosa*. There are also areas of *Calluna* and *Pteridium*. There is no woodland on the island, which is surrounded by sea and is 8 km from the nearest area of trees on the mainland. However, there is evidence that trees grew between the current west coast of Wales and offshore islands before isostatic rebound in the mid-Holocene when the area was a land bridge (Evans, 1986, Bell, 2007, UKHO, 2011). Moreover, the name of a nearby island, Skokholm, is thought to mean “wooded isle” (Morgan, 1887). The presence of abundant *H. non-scripta* has been previously interpreted as evidence of past woodland on the island (e.g.

Evans, 1986). Palynological study from a wet depression on the island by Webb et al. (2017) has provided a detailed profile of the vegetation community between 2,840 Cal. BP and the present day. Within this period, the vegetation community has alternated between heath dominated by Ericaceae and grassland dominated by Poaceae, with Cyperaceae and *Rumex* appearing variably throughout and arboreal pollen (*Alnus*, *Betula*, *Fraxinus*, *Pinus*, *Quercus*, *Tilia* and *Ulmus*) accounting for ~5% of the total pollen sum. This is likely to be a minor regional signal, especially given the range of species involved and the very small quantities represented. Given the submerged trees between the mainland and island, it is likely that woodland was present before 2,840 Cal. BP but it was not possible to establish this definitely due to the Mesolithic period being absent in the core record. Interestingly, though, *Hyacinthoides* was present in the core before 2,840 Cal. BP. This insect-pollinated species has been only rarely recorded in sediments in northwest Europe and is generally under-represented (Waller et al, 2012). Modern vegetation surveys have revealed an extremely rich AWI flora, with 74 species represented. This makes Skomer Island second only to Sydlings Copse in total AWI species present, which has been wooded continuously since 1,000 Cal BP (75 species), and slightly above Garbutt Wood, which has been wooded continuously since 1,400 Cal BP (72 species).

It is notable that all three sites contain heathland plants, especially *Calluna* and *Pteridium*, which are present at three sites and two sites, respectively. It is possible that species such as these act to form a surrogate woodland canopy. This possibility is also supported by analysis of an undated core at Winding Stonard Wood in the New Forest, Hampshire by Dimbleby and Gill (1955), which showed that arboreal pollen was only found in high quantities (>20%) in the top 5-10 cm of the core; below that Ericaceae was dominant almost to the exclusion of any other taxa (~70%). It seems likely that this site has only fairly recently supported woodland and yet it supports 13 AWI species including two strong species: *Ruscus aculeatus* and *O. acetosella*. This suggests either that these species have colonised unusually rapidly or, as seems more probable, were able to exist on the site before the current woodland was present.

4. Conclusions and Recommendations

This study provides the first account of palynology being used to critique the concept and robustness of AWIs across multiple sites. Analysis of vegetation at the species-rich Derrycunihy Wood and the species-poor Wistman's Wood lends support to the concept that sites *proven* to support ancient woodland based on palynology (rather than being declared ancient based on patchy, inaccurate or imprecise historical records or cartographic evidence), can support good AWI species communities. This remains the case even if the woodland is species-poor, although AWI richness is reduced. However, the high number of AWIs at sites with interrupted woodland – Garbutt Wood, Sydlings Copse, Piles Copse, Johnny

Wood and Oxborough Wood – suggests that AWI species : (1) are more resilient to interruptions than often believed; or (2) recolonise more quickly than expected following interruptions. Moreover, analysis of three clear-felled sites – Hartlebury, Gunnister and Skomer – shows that prominent, and sometime rich, AWI communities can occur despite sites not having been wooded for at least 2,700 years. This indicates that some, possibly many, AWI species have greater tolerance of non-woodland conditions than is often believed and thus a greater persistence following deforestation.

As regards resilience to interruptions, it is possible that some species are surviving in the seed banks during woodland hiatus. This conjecture is supported by the presence of *Mercurialis perennis* pollen – one of the very few AWI species that can be identified to species level in a core using pollen morphology – in the palynological profile of Sydlings Copse (Day, 1993). The species occurs sporadically after the interpolated date of 3,600 Cal. BP whenever arboreal pollen is abundant, is absent during the woodland interruption, and finally reappears at about 600 Cal. BP after an absence of 700 years. For other AWI species, there is evidence to indicate that AWIs can (re)colonise quickly. For example, also at Sydlings Copse, *A. nemorosa* has only occurred within the last 600 years (i.e. after the hiatus), suggesting it might have colonized at this time. However, as the preservation of *A. nemorosa* pollen is unknown we cannot totally discount the possibility that it is not present <600 Cal. BP due to degradation of the fossilised pollen grain rather than being truly absent from the core. With any of the interrupted sites, it is important to note that the temporary decreases in the abundance of arboreal pollen could feasibly be driven by a period of active coppice management rather than a genuine woodland interruption. However, the impact of coppicing on pollen records in woodland settings has been considered by Waller et al., (2012) and Bunting et al., (2016) and concluded that coppicing has little or no impact on pollen production. We can thus be confident that periods interpreted as woodland interruptions are likely to be just are clearance events, even those that are very short (e.g. Oxborough and Johnny Wood). This interpretation is strengthened by the fact that all tree species are lost from the pollen record during these times rather than simply the species that would typically be coppiced.

Regardless of past woodland stability, previous interruptions, or contemporary clearance, the number of AWIs in any species community links to its overall species richness. For example, the interrupted species-poor woodland at Piles Copse supported just 12 AWI species in comparison with interrupted species-rich sites, Sydlings Copse and Garbutt Wood, which support 75 and 72 AWIs, respectively. It was also interesting to note that although the area of a site might influence species number (and thus AWI number and likelihood of ancient woodland classification),

a simple calculation of total number of AWI species divided by the size for each of our locations ranked Skomer (currently non-wooded) similarly to Derrycunihy Wood (a proven continuously wooded site). This suggests that although Swallow and Goodenough (2017) note that edge sites yield fewer AWI species, and therefore imply that small fragmented ancient woodlands support fewer AWI species, the overall species richness might be a bigger influence.

This research suggests that defining ancient woodland areas needs to be revisited. Points for consideration are:

- 1) **Utilising palaeoecological evidence:** This study has demonstrated that palynology can provide robust data on woodland history continuity. When coupled with radiocarbon dating, any interruptions can be dated to provide objective empirical evidence upon which to base ancientness classification decisions. However, palynological profiling is by no means a “silver bullet”: the amount of time needed to process a core, identify and count pollen within the different layers, and obtain radiocarbon dates is very considerable. The process also requires specialist laboratory facilities and substantial experience. As such, it is unlikely that palynological profiling will become a regular feature of ancientness assessment – except perhaps at the most important or complex sites – and it is thus vital to improve the current AWI system by considering the points below.
- 2) **Weighting AWI species to create a biotic index:** As many species currently designated as AWIs have been shown in this study to occur in non-woodland habitats, it would be prudent to review lists to weight species typically only found in continuously-wooded areas more highly than those that can be found elsewhere. This concept is similar to highlighting strict/strong AWIs (as per Rackham, 2003), but could be developed by explicitly factoring weighting into AWI lists to create a numerical biotic index. Such an index might be similar, for example, to Chandler’s score for invertebrates to assess water quality (Chandler, 1970) and could replace the current AWI biosurvey approach, which is based on simple species lists. In essence, the species rated most highly would be those that occur exclusively in continuous ancient woodland. Based on the data in this study, very few AWI species occurred exclusively in such sites relative to interrupted woodland or recently-cleared woodland. The two exceptions were *Atrichum undulatum* and *Salix aurita*, but this was probably more to do with site-specific environmental conditions than the fact that these are true indicator species. However, several of the species occurred only in continuously-wooded and interrupted woodlands. Some of these species had already been identified by Rackham (2003) as strict or strong AWI species and included *E. amygdaloides*, *H. hirsutum*, *L. nemorum* and *P. quadrifolia*, but others are new including *Lysimachia vulgaris*, *O. acetosella*, *Stellaria holostea* and *Valeriana officinalis*. Such species could be given a high

score in a putative AWI biotic index. Species that rely on branched rhizomes for reproduction are thus very slow dispersers such as *A. nemorosa* (Brunet and von Oheimb, 1998), but which appear tolerant of periods of disturbance based on their presence in our interrupted woodland sites, could be given an intermediate score. Finally, species with a low habitat specificity, such as *Galium saxatile* and *Lonicera periclymenum*, would be given a low score, together with species displaying persistence traits noted by Peterken (1974) and Vallet et al., (2010): higher specific leaf area, rosette or semi-rosette form, reliant on seed dispersal (particularly 'light' seeds) rather than underground rhizome regeneration, affinity for base-rich and fertile soils, and short life-spans.

- 3) **Reverse indicators:** To date, the focus of classifying between ancient and recent woodland has been based upon species that occur in the former. Another option would be to develop lists of species that occur predominantly in recent woodlands (e.g. species that are disturbance specialist) on the basis that, if these were absent from a site, it might indicate that a site was ancient. This could either become a companion list to the AWI list or the concept could be integrated into a numerical biotic index using negative weightings. Such species might include *Chamaenerion angustifolium*, *Plantago lanceolata* and *Urtica dioica*.
- 4) **Threshold number of species:** Given the high number of AWIs found at non-ancient sites, we suggest that the number of species present at a site before it is designated ancient should be increased. Consideration should also be given to having a relative threshold (e.g. 10% of species present at a site being AWIs) rather than an absolute threshold. To some extent, this would also address the current inconsistency between local lists and thus the spatial variation in the ease with which a site can be designated as ancient. For example, the Leicestershire and Rutland list contains 18 AWIs whereas Derbyshire has 123 (Glaves, 2009) but the two areas are of similar size (2.2 km² and 2.4 km², respectively). Although some of this variation will be due to genuine differences, it would appear to be harder for a site to be designated as an AWI in some counties relative to others if only the local list is used. Even if this relative system is adopted, work to rebalance local lists is recommended to reduce spatial differences in ancientness assessment while retaining the concept that some AWI species are important in a local context only (e.g. *H. non-scripta*, which is a genuine AWI in some areas, but associated with grassland, heath, scrub, hedge banks and sea cliffs in others: Preston, et al, 2002).
- 5) **Moving from within-taxon to between-taxa indicators:** Finally, although within-taxon community indicator approaches are stronger than single-species approaches (diatoms, Rimet, 2015; lichens, Llop et al., 2012), we suggest that, in the case of ancient woodland, a between-taxa system should be considered. This might

incorporate fungi, lichens and beetles, which have previously been used in isolation as ancient woodland indicators (e.g. Bredesen, 1997; Coppins and Coppins 2002; Humphrey, 2002; Sroka, 2006) to create a multi-taxa system, as suggested previously for Italy (Blasi et al., 2010). The value of this approach has already been highlighted in this study in the case of Wistman's Wood (see above). Such expansions would, of course, have implications on the amount of survey effort needed in future surveys, but given that cross-taxa data are already in existence for many sites, adding non-plant taxa into a numerical biotic index might at least be worthy of consideration going forward.

4.1 Final thoughts

Fundamentally, the aim of conservationists globally is to preserve ancient woodland for its unique biodiversity. Many of the vascular species that grow in these old growth forests have slow dispersal mechanisms and/or rely heavily upon the woodland structure for survival. Protection of these woodland settings is therefore essential for the continual success of these diverse and rich environments.

As pointed out by Rotherham (2011), defining exactly what AWIs actually 'indicate' is hugely important but is often overlooked. Many so-called indicators of ancient woodland sites might actually simply be plants of undisturbed ground. Indeed, it is notable that a number of the AWI species present at the three sites that are not currently wooded - Hartlebury, Gunnister and Skomer - have been found previously to be indicative of long-established habitats but not necessarily long-established woodland (Rackham, 2003). For example, *Conopodium majus*, *Orchis mascula*, and *Primula vulgaris* are all found on Skomer; all of which can be found in old grassland habitats. Moreover, some of species considered to be woodland specialists by virtue of their need for shelter and high humidity seem to be tolerant of non-woodland locations if these can be provided by a surrogate canopy (*Pteridium* on Skomer, for example). From a more philosophical perspective, it could also be argued that a high number of AWIs link to conservation value in two ways: (1) AWI species themselves are often rare and declining; and (2) their presence indicates an area is relatively undisturbed and non-fragmented, two factors that increase ecological value and conservation priority.

By critiquing the method of indicator species in this paper and demonstrating the weakness of the technique we are not attempting to reduce the number of woodlands currently assigned as ancient, nor are we suggesting that the species approach is not useful. However, it is vital that practitioners understand the limitations of the technique and to highlight the need for a standard approach to ancient woodland status allocation.

Acknowledgements

For their help in supplying vegetation data and site records, we thank Martin Longley, Andy Nisbet, Albert Knott, and Matthew Parker (Natural England), Claire Wood (Centre for Ecology and Hydrology), Phillip Whelpdale (Yorkshire Wildlife Trust), Helen Baczkowska and Emily Nobbs (Norfolk Wildlife Trust), Mark Bradfield (Berkshire, Buckinghamshire and Oxfordshire Wildlife Trust), Birgitta Büche and Ed Stubbings (Skomer National Nature Reserve wardens), Peter Jarvis (Birmingham Natural History Society), Gill Smith and Tom Denney (Ryedale Naturalists), Roger Maskew (Hartlebury Common Local Group) and John Howell. We also thank Oliver Moore for checking species and vernacular names.

References

- Baker, C. A., Moxey, P. A., Oxford, P. M., 1978. Woodland continuity and change in Epping Forest. *Field Studies*, 4, 645-669.
- Barkham, J.P., 1992. The effects of management on the ground flora of ancient woodland, Brigsteer Park Wood, Cumbria, England. *Biological conservation*, 60(3), 167-187.
- Bell, M., 2007 Prehistoric coastal communities: the Mesolithic in western Britain. *CBA Research Reports*
- Bennett, K. D., Boreham, S., Hill, K., Packman, S., Sharp, M. J., Switsur, V. R., 1993. Holocene environmental history at Gunnister, north Mainland, Shetland. *The Quaternary of Shetland: Field Guide*. Cambridge: Quaternary Research Association, pp.83-98.
- Bennett, K. D., Bunting, M. J., Fossitt, J. A., 1997. Long-term vegetation change in the Western and Northern Isles, Scotland. *Botanical Journal of Scotland*, 49(2), 127-140.
- Birks, H. J. B., 1993. Quaternary palaeoecology and vegetation science - current contributions and possible future developments. *Review of Palaeobotany and Palynology* 79, 153-177.
- Birnie, J., 1984. Trees and Shrubs in the Shetland Islands: Evidence for a Postglacial Climatic Optimum? In: *Climatic Changes on a Yearly to Millennial Basis* Springer Netherlands.
- Blackham, A., Davies, C., Flenley, J., 1981. Evidence for late Devensian landslipping and late Flandrian forest regeneration at Gormire Lake, North Yorkshire. The Quaternary in Britain: essays, reviews and original work on the Quaternary published in honour of Lewis Penny on his retirement, 184.
- Blasi, C., Marchetti, M., Chiavetta, U., Aleffi, M., Audisio, P., Azzella, M.M., Brunialti, G., Capotorti, G., Del Vico, E., Lattanzi, E. and Persiani, A.M., 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. *Plant Biosystems*, 144, 160-170.
- Bradshaw, R. H., 1981. Quantitative reconstruction of local woodland vegetation using pollen analysis from a small basin in Norfolk, England. *The Journal of Ecology*, 941-955.
- Bradshaw, R. H., Jones, C. S., Edwards, S. J., Hannon, G. E., 2015. Forest continuity and conservation value in Western Europe. *The Holocene*, 25(1), 194-202.
- Bredesen, B., Haugan, R., Aanderaa, R., Lindblad, I., Økland, B., Røsok, Ø., 1997. Wood-inhabiting fungi as indicators of ecological continuity within spruce forests of southeastern Norway. *Blyttia* (Oslo) 54, 131-140 (in Norwegian with English summary).
- Brown, A. G., 1984. The Flandrian vegetational history of Hartlebury Common, Worcestershire. In: *Proceedings Birmingham Natural History Society* 25 (2) 89-98
- Brown, A. D., 2010. Pollen analysis and planted ancient woodland restoration strategies: a case study from the Wentwood, southeast Wales, UK. *Vegetation History and Archaeobotany*, 19(2), 79-90.
- Brunet, J., von Oheimb, G., 1998, Colonization of secondary woodlands by *Anemone nemorosa*. *Nordic Journal of Botany*, 18, 369-377
- Bryant, V.M., Holloway, R.G., 1983. The role of palynology in archaeology. *Advances in archaeological method and theory*. 6, 191-224.

- Buchanan White, F., 1898. *The Flora of Perthshire*. Edinburgh
- Bunting, M. J., Grant, M. J., Waller, M., 2016. Pollen signals of ground flora in managed woodlands. *Review of Palaeobotany and Palynology* 224, 2, 121-133
- Bunting, M.J., Gaillard, M-J., Sugita, S., Middleton, R. and Broström, A., 2004. Vegetation structure and pollen source area. *The Holocene*, 14, 651–660.
- Chandler, J.R., 1970. A biological approach to water quality management. *Water Pollution Control*, 4, 415–422
- Chapman, J., André, P., 1777. A Map of the County of Essex from an Actual Survey taken in MDCCLXXII, :LXXIII and MDCCLXXIV.
- Coppins, A.M., Coppins, B.J., 2002. Wistman's Wood NNR, cSAC, (VC 3, South Devon): Desk Study - to discover relevant information relating to past and present site history and management and the history of lichen recording prior to carrying out a lichen survey. English Nature, Exeter.
- Coppins, B.J., Coppins, A.M., 2005. Lichens – The biodiversity value of western woodlands. *Botanical Journal of Scotland* 57 (1–2), 141–153.
- Day, S. P., 1993. Woodland origin and 'ancient woodland indicators': a case-study from Sidlings Copse, Oxfordshire, UK. *The Holocene*, 3(1), 45-53.
- De Keersmaeker, L., Martens, L., Verheyen, K., Hermy, M., De Schrijver, A., Lust, N., 2004. Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen forest (Belgium) *Forest Ecology and Management* 188(1–3), 291-304
- Dimbleby, G. W., Gill, J. M., 1955. The occurrence of podzols under deciduous woodland in the New Forest. *Forestry*, 28(2), 95-106.
- Durham County Council, 2008. The County Durham Landscape Guidelines: Woodland and Forestry, Durham County Council.
- Dzwonko, Z., 1993. Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. *Journal of Vegetation Science*, 4, 693–698.
- Evans, J. G., 1986. Prehistoric farmers of Skomer Island: An archaeological guide. In: *Nature conservation*. Dyfed: West Wales Trust. pp.13-14.
- Fægri, K., Iversen, J., 1964 *Textbook of Pollen Analysis*. Scandinavian University Books: Munksgaard
- Forman, R.T.T., 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press
- Glaves, P., Handley, C., Birbeck, J., Rotherham, I., Wright, B., 2009. A survey of the coverage, use and application of ancient woodland indicator lists in the UK.
<http://nrl.northumbria.ac.uk/3467/1/Glaves%2C%20Rotherham%2C%20Wright%2C%20Handley%2C%20Birbeck%20-%20A%20survey%20of%20the%20coverage%2C%20use%20and%20application%20of%20ancient%20woodland...%20Report.pdf>
- Goldberg, E., Kirby, K., Hall, J., Latham, J., 2007. The ancient woodland concept as a practical conservation tool in Great Britain. *Journal for Nature Conservation*, 15(2), 109-119.
- Grant, M. J., Edwards, M. E., 2008. Conserving idealized landscapes: past history, public perception and future management in the New Forest (UK). *Vegetation History and Archaeobotany*, 17(5), 551-562.

- Grashof-Bokdam, C., 1997. Colonization of forest plants: the role of fragmentation. IBN Scienti[®]c Contributions 5, Wageningen.
- Hardy, M.B., Hurt, C.R., Bosch, O.J.H., 1999. Veld condition assessment. - In: Tainton N (ed.), *Veld management in South Africa*. Pietermaritzburg: University of Natal Press, pp 194–216.
- Hasselbach, L., Ver Hoef, J.M., Ford, J., Neitlich, P., Crecelius, E., Berryman, S., Wolk, B., Bohle, T., 2005. Spatial patterns of cadmium and lead deposition on and adjacent to National Park Service lands near Red Dog Mine, Alaska. *Science of the Total Environment*, 348, 211-238.
- Hellman, S., Bunting, M.J., Gaillard, M.-J., 2009. Relevant Source Area of Pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: A simulation approach. *Review of Palaeobotany and Palynology* 153, 245–258.
- Hermly, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, 91(1), pp.9-22.
- Hodge, S.J. Peterken, G.F., 1998. Deadwood in British Forests: Priorities and a Strategy. *Forestry*. 71 (2), 99 - 112
- Honnay, O., Degroote, B., Hermly, M., 1998. Ancient-forest plant species in Western Belgium: a species list and possible ecological mechanisms. *Belgian Journal of Botany* 130, (2), 139-154.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., Hermly, M., 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5 (4), 525-530.
- Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biological Conservation*, 107(2), pp.165-180.
- Jacquemyn, H., Butaye, J., Hermly, M., 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography*, 28(6), 801-812.
- Johansen, J. 1975. Pollen diagrams from the Shetland and Faroe Islands. *New Phytologist*, 75(2), 369-387.
- Kelly, D. L. 1981. The native forest vegetation of Killarney, south-west Ireland: an ecological account. *Journal of Ecology*, 69, (2) 437-472.
- Kimberley, A., Blackburn, G. A., Whyatt, J. D., Kirby, K., Smart, S. M., 2013. Identifying the trait syndromes of conservation indicator species: how distinct are British ancient woodland indicator plants from other woodland species? *Applied Vegetation Science*, 16 (4), 667.
- Kirby, K. J., Goldberg, E., 2002. *Ancient woodland: guidance material for local authorities*. English Nature, Peterborough
- Kirby, K.J., Reid, C.M., Isaac, D., Thomas, R.C., Watkins, C., 1998. The ancient woodland inventory in England and its uses. In: *The ecological history of European forests* pp. 323-336. CAB International, Oxford
- Landres, P. B., Verner, J., Thomas, J. W., 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2, 316–328.
- Llop E., Pinho, P., Matos, P., Pereira, M.J., Branquinho, C., 2012. The use of lichen functional groups as indicators of air quality in a Mediterranean urban environment. *Ecological Indicators*, 13, 215-221

- Marcot, B.G., Croft, L.K., Lehmkuhl, J.F., Naney, R.H., Niwa, C.G., Owen, W.R., Sandquist, R.E., 1998. Macroecology, paleoecology, and ecological integrity of terrestrial species and communities of the interior Columbia basin and northern portions of the Klamath and Great Basins. Interior Columbia Basin ecosystem management project: scientific assessment. Report PNW-GTR-410. U.S. Forest Service, Oregon.
- McCarroll, J., Chambers, F. M., Webb, J. C., Thom, T., 2015. Application of palaeoecology for peatland conservation at Mossdale Moor, UK. *Quaternary International* 432 (A) 39 - 47
- McGeoch, M. A., 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews of the Cambridge Philosophical Society* 73, 181–201.
- Mitchell, F. J. G., 1988. The vegetational history of the Killarney oakwoods, SW Ireland: evidence from fine spatial resolution pollen analysis. *Journal of Ecology*, 76 (2) 415-436.
- Morgan, T., 1887. Handbook of the origin of place-names in Wales and Monmouthshire. Available online http://lennatur.com/files/u1/on_Place-names_ThosMorgan_Pr_HWSouthey_1887.pdf (accessed 1.8.14)
- Nilsson, S.G., Hedin, J., Niklasson, M., 2001. Biodiversity and its assessment in boreal and nemoral forests. *Scandinavian Journal of Forest Research*, 16 (S3), 10-26.
- Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation*, 10 (5), 779-791.
- Ohlson, M., Söderström, L. Hörnberg, G. Zackrisson, O., Hermansson, J., 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation* 81, 221–231.
- Oldfield, F., Wake, R., Boyle, J., Jones, R., Nolan, S., Gibbs, Z., Appleby, P., Fisher, E., Wolff, G., 2003. The late-Holocene history of Gormire Lake (NE England) and its catchment: a multiproxy reconstruction of past human impact. *The Holocene*, 13(5), 677-690
- O'Sullivan, A., Kelly, D. L., 2006. A recent history of sessile oak (*Quercus petraea* (Mattuschka) Liebl.)-dominated woodland in Killarney, SW Ireland, based on tree-ring analysis. *Biology and Environment: Proceedings of the Royal Irish Academy*, 106B (3) 355-370.
- Palo, A., Ivask, M., Liira, J., 2013. Biodiversity composition reflects the history of ancient semi-natural woodland and forest habitats – complication of an indicator complex for restoration practice. *Ecological Indicators* 34, 336-344
- Peterken, G. F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology*, 72 (1), 155-182.
- Peterken, G.F., 1974. A method of assessing woodland flora for conservation using Indicator Species. *Biological Conservation*, 6, 239-245.
- Peterken, G.F., 1981. *Woodland Conservation and Management*. Chapman and Hall, London.
- Petersen, P.M., 1994. Flora, vegetation, and soil in broadleaved ancient and planted woodland, and scrub on Rønne, Denmark. *Nordic Journal of Botany* 14, 693-709.
- Proctor, M. C. F., 1962. The epiphytic bryophyte communities of the Dartmoor oak woods. *Transactions of the Devon Association for the Advancement of Science*, 94, 531-554.

- Rackham, O., 1986. *The History of the Countryside*. Dent, London
- Rackham, O., 2003. Ancient woodland, its history, vegetation and uses in England. Ancient woodland, its history, vegetation and uses in England (revised edition). Castlepoint Press, Dumfries
- Ratcliffe, D. A., 1968. An ecological account of Atlantic bryophytes in the British Isles. *The New Phytologist*, 67 (2), 365-439.
- Rimet, F., Bouchez, A., Montuelle, B., 2015. Benthic diatoms and phytoplankton to assess nutrients in a large lake: Complementarity of their use in Lake Geneva (France–Switzerland), *Ecological Indicators*, 53, 231-239
- Roberts, C. A., Gilbertson, D. D., 1994. The vegetational history of Pile Copse ancient oak woodland, Dartmoor, and the possible relationships between ancient woodland, clitter, and mining. *Proceedings of the Ussher Society*, 8, 298-298.
- Rolstad, J., Gjerde, I., Gundersen, V.S., Sætersdal, M., 2002. Use of indicator species to assess forest continuity: a critique. *Conservation Biology*, 16, (1), 253-257.
- Rose, F., Coppins, A.M., 2002. Site Assessment of Epiphytic Habitats using Lichen Indices. In: Nimis, P.L., Scheidegger, C., Wolseley, P.A. (eds) *Monitoring with Lichens - Monitoring Lichens*, 7, 343–348. Kluwer Academic Publishers, Dordrecht
- Rose, F., 1976. Lichenological indicators of age and environmental continuity in woodlands. In: Brown, D.H., Hawksworth, D.L., Bailey, R.H. (eds), *Lichenology: Progress and Problems*, 278–307. Academic Press, London.
- Rotherham, I. D., 2011. *A landscape history approach to the assessment of ancient woodlands. Woodlands: ecology, management and conservation*, Nova Science Publisher, New York
- Rotherham, I.D., Jones, M., Smith, L., Handley, C. (Eds.) 2008. *The Woodland Heritage Manual: A Guide to Investigating Wooded Landscapes*. Wildtrack Publishing, Sheffield.
- Schmidt, M., Mölder, A., Schönfelder, E., Engel, F., Schmiedel, I., Culmsee, H., 2014. Determining ancient woodland indicator plants for practical use: A new approach developed in northwest Germany. *Forest Ecology and Management*, 330, 228-239
- Scott, W., Palmer, R., 1987. *The flowering plants and ferns of the Shetland Islands*. Shetland Times Ltd, Lerwick
- Simmons, I.G., 1965. The Dartmoor oak copses: observations and speculations. *Fields Studies* 2, 225-235.
- Spencer, J. W., Kirby, K. J., 1992. An inventory of ancient woodland for England and Wales. *Biological Conservation*, 62 (2), 77-93.
- Spencer, J., 1990. Indications of antiquity: some observations of the nature of plants associated with ancient woodland. *British Wildlife*, 2, 90-102
- Sroka, K., Finch, O.D., 2006. Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation*, 10(4), 335-350.
- Stefańska-Krzaczek, E., Kacki, Z., Szygula, B., 2016. Coexistence of ancient forest species as indicators of high species richness. *Forest Ecology Management*. 365, 12-21

- Sugita, S., 1994 Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology*, 82, 881–897.
- Sugita, S., Gaillard, J., Broström, A., 1999. Landscape openness and pollen records: a simulation approach. *The Holocene* 9, 409–421.
- Swallow, K., Goodenough, A.E., 2017. Double-edged effect? Impact of dual edge proximity on the distribution of ancient woodland indicator plant species in a fragmented habitat. *Community Ecology*, In Press.
- The Woodland Trust, 2007. Back on the Map: An inventory of ancient and long-established woodland for Northern Ireland. Available from: www.backonthemap.co.uk (accessed 26.10.2016)
- Tzedakis, P.C., Andrieu, V., De Beaulieu, J.L., Crowhurst, S.D., Follieri, M., Hooghiemstra, H., Magri, D., Reille, M., Sadori, L., Shackleton, N.J., Wijmstra, T.A., 1997. Comparison of terrestrial and marine records of changing climate of the last 500,000 years. *Earth and Planetary Science Letters*, 150 (1), 171-176.
- UKHO (2011) INSPIRE Portal and Bathymetry DAC. Available from: <http://aws2.caris.com/ukho/mapViewer/map.action> (accessed: 31.8.2016)
- Vallet, J., Daniel, H., Beaujouan, V., Rozé, F., Pavoine, S., 2010. Using biological traits to assess how urbanization filters plant species of small woodlands. *Applied Vegetation Science*, 13 (4), 412-424.
- Vera, F.W.M., 2000. *Grazing ecology and Forest History*. CABI Publishing, Wallingford
- Waller, M., Grant, M. J., Bunting, M. J., 2012. Modern pollen studies from coppiced woodlands and their implications for the detection of woodland management in Holocene pollen records. *Review of Palaeobotany and Palynology*. 187, 11-28.
- Webb, J.C., MCCarroll, J., Carpenter, W., Chambers, F.M., Toms, P.S., Wood M.J., (2017) Apparent lack of woodland and relative abundance of woodland indicator species: the role of humans, birds and rabbits in the changing vegetation of Skomer Island, Wales. *Archaeology in Wales* [In Press].
- Wells, R.W., Lertzman, K.P., Saunders, S.C., 1998. Old Growth Definitions for the Forests of British Columbia, Canada. *Natural Areas Journal* 18 (4), 280-294
- West, S., 1997. Geochemical and Palynological Signals for Palaeoenvironmental Change in South West England. PhD. Thesis, University of Plymouth
- Wulf, M., 1997. Plant species as indicators of ancient woodland in northwestern Germany. *Journal of vegetation Science*, 8 (5), 635-642.
- Xu, Q., Zhang, S., Gaillard, M., Li, M., Cao, X., Tian, F., Li, F., 2016. Studies of modern pollen assemblages for pollen dispersal- deposition- preservation process understanding and for pollen-based reconstructions of past vegetation, climate, and human impact: A review based on case studies in China. *Quaternary Science Reviews*, 149 151-166.
- Zacharias, D., 1994. Bindung von Gefäßsporenanzeigen an Wälder alter Waldstandorte im nördlichen Harzvorland Niedersachsens - ein Beispiel für die Bedeutung des Alters von Biotopen für den Pflanzenschutz. *Norddeutsche Naturschutzakademie-Berichte* 94, (3) 76- 88.

Table 1: Details of sites used in this metastudy and the sources of palynological information.

Study sites	County	Latitude and longitude	Study site (ha)	Source of palynological information
Derrycunihy Wood	Kerry	51.9933, -9.5572	136	Mitchell (1988)
Wistman's Wood	Devon	50.5812, -3.9576	3	Bradshaw et al. (2015)
Garbutt Wood	Yorkshire	54.2422, -2.2293	54	Blackham et al. (1981) Oldfield et al. (2003)
Sydlings Copse	Oxfordshire	51.7814, -1.1953	22	Day (1993)
Piles Copse	Devon	50.4441, -3.9094	50	Roberts and Gilbertson (1994) West (1997)
Johnny Wood	Cumbria	54.5199, -3.1611	37	Birks (1993)
Oxborough Wood	Norfolk	52.5857, 0.5462	23	Bradshaw (1981)
Hartlebury Common	Worcestershire	52.3323, -2.2582	90	Brown (1984)
Gunnister	Shetland	60.4515, -1.4124	6	Bennett (1997)
Skomer Island	Pembrokeshire	51.7376, -5.2960	292	Webb et al. (2017)
Winding Stonard Wood	Hampshire	50.8490, -1.4354	2	Dimbleby and Gill (1955)

Table 2. Ancient woodland indicator species presence at study sites as determined using Glaves et al., (2009), The Woodland Trust (2007), Durham County Council (2008) and Peterken (1974). Species with strict or strong association to ancient woodland as per Rackham (2003).

Plant type	AWI type	Proven continuous woodland		Interrupted woodland					Not currently woodland			Woodland on old heath
		Derrycunihy Wood	Wistman's Wood	Garbutt Wood	Sydlings Copse	Piles Copse	Johnny Wood	Oxborough Wood	Hartlebury Common	Gunnister	Skomer Island	Winding Stonard Wood
Trees	Local	0	0	3	2	0	0	0	0	0	1	0
	Total	3	5	8	3	2	4	2	3	0	2	2
Woody	Local	0	0	1	0	0	0	0	0	0	1	0
	Strict/strong	0	0	0	0	0	0	0	0	0	0	1
	Total	5	6	9	7	2	5	2	2	2	5	6
Forbs	Local	2	0	10	8	0	2	3	1	0	9	0
	Strict/strong	2	1	3	7	1	3	0	0	0	0	1
	Total	6	6	50	51	2	23	9	11	6	52	3
Graminoid	Local	2	1	0	9	0	2	0	1	1	1	0
	Strict/strong	0	0	0	5	0	2	0	0	0	0	0
	Total	3	5	2	14	2	5		4	5	7	2
Non-flowering	Local	1	0	0	0	0	0	0	0	0	1	0
	Total	11	12	3	No data	4	9	No data	1	7	8	No data
Overall	Local	5	1	14	19	0	4	3	2	1	13	0
	Strict/strong	2	1	3	12	1	5	0	0	0	0	2
	Total	28	34	72	75	12	46	13	21	20	74	13



Figure 1. Location of main study sites (black text) and additional sites (grey text).

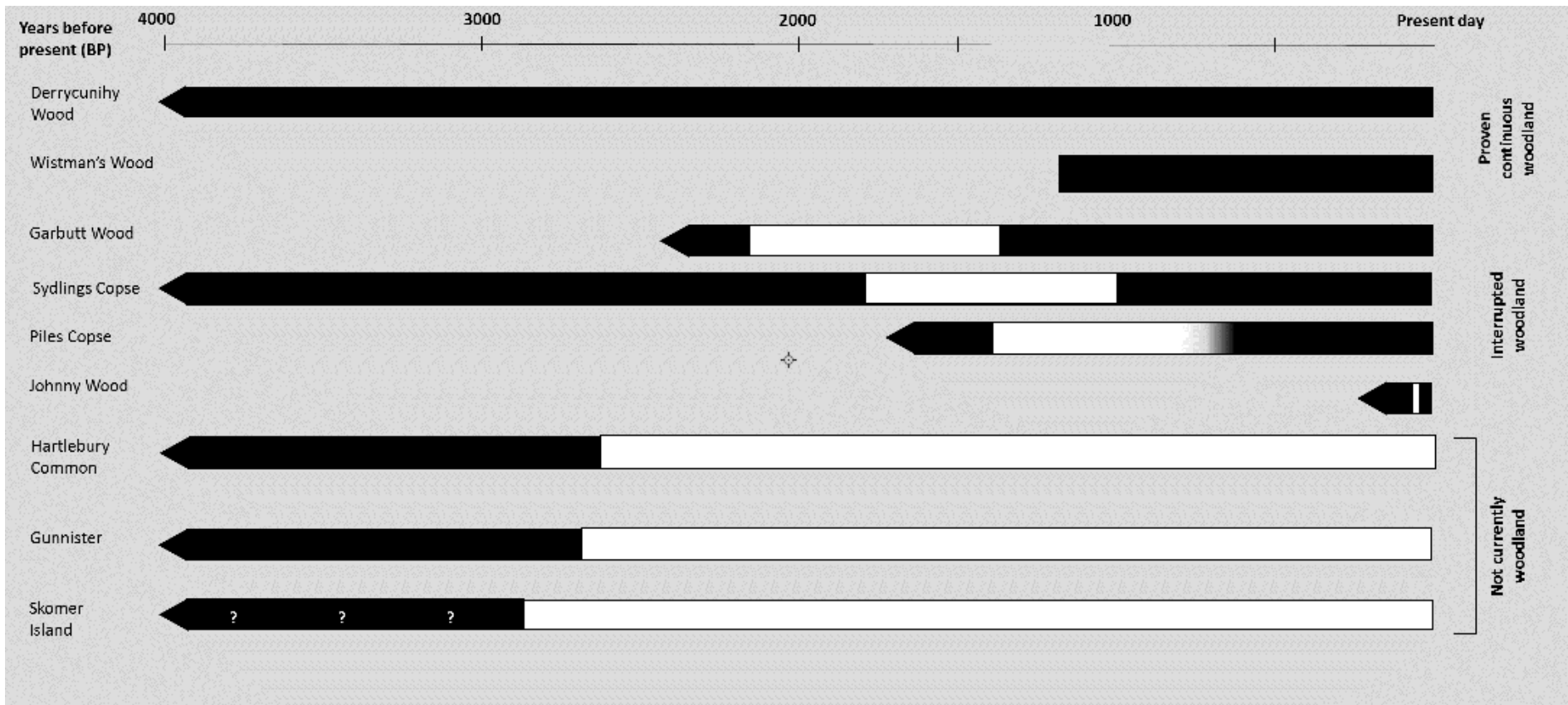


Figure 2. Timeline of woodland continuity for each study site. Black bars indicates proven woodland coverage, except where overlain by a question mark. White bars indicate periods of woodland interruption or clearance. Instances where the sediment core continues beyond dated horizons are indicated with a left arrow.