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Reprint of "Long-term changes and drivers of biodiversity in Atlantic oakwoods"

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ABSTRACT

Atlantic oakwoods are of high conservation value in western Europe. Developing effective conservation management policies requires data on the dynamics of woodland over long time scales. Such data are not available through monitoring or documentary records so palaeoecological data have been investigated. Pollen and charcoal data from four western Irish woods covering up to 7000 years have been analysed to provide information on changes in alpha and beta diversity, rates of change and fire history over time. These analyses reveal that the most significant changes in biodiversity relate to the loss of *Pinus sylvestris* from these woods followed by their exploitation and subsequent management for timber, charcoal and tan bark. The structure and composition of the present day woods still display a strong legacy from their exploitation and this raises important questions relating to the long-term conservation management of these woods.

1. Introduction

The Atlantic oakwoods of western Europe have been regarded as temperate rainforest due to the high degree of oceanicity that they enjoy and the associated richness and luxuriance of their bryophyte and fern floras (Baarda, 2005; Kelly, 2005). They have distinctive biodiversities (Hall and Stone, 2005; Kelly, 2005) and consequently are listed as Annex 1 habitats (EU code 91A0) under the European Union's Habitats Directive (E.U., 1992) which affords their protection under national conservation designations in the relevant countries. Atlantic oakwoods have been developing throughout the postglacial (Brewer et al., 2005). Although they are defined by their oceanic climate, palaeoecological evidence from Ireland, Scotland and Wales demonstrates that they have been profoundly influenced by human impacts in the past (Edwards, 1986; Mitchell, 1988, 1990; Little et al., 1996; Sansum, 2004). Vegetation surveys have also highlighted disturbance in the form of grazing and timber extraction as being the principal drivers of structural changes to Atlantic oakwoods throughout Britain as well as in the Basque country of Northern Spain (Onaindia et al., 2004; Amar et al., 2010). Both climate change and human induced impacts are identified as significant threats to the future continuity of this conservation resource (Hall and Stone, 2005; Kelly, 2005).

Addressing the mitigation of these threats requires the investigation of long-term data that cover temporal scales that are commensurate with that of the forest cycle of tree generations. Although some long-term monitoring datasets do exist (Silvertown et al., 2010) they are never of sufficient quality or longevity to address the dynamics of forest successions. Despite this, Keith et al. (2009) have used long-term data to demonstrate taxonomic homogenization of woodland communities in southern England over a 70 year period. Additionally, resurveys of British woodlands after two to four decades have revealed structural changes associated with a range of drivers that vary in both space and time (Peterken and Jones, 1987, 1989; Kirby et al., 2005; Mihok et al., 2009; Amar et al., 2010). These investigations raise the question of how much the biodiversity of Atlantic oakwoods has been impacted by the human exploitations that they suffered in recent centuries or indeed by the non-intervention conservation policies that have been adopted in recent decades. Detailed floristic data covering these times, as well as from earlier, to provide a baseline do not exist but some relevant information can be obtained from palaeoecological sources (Mitchell, 2011).

Pollen analysis has the advantage that long time records (thousands of years) of vegetation change can be reconstructed from a single site. The main restriction of this approach is poor spatial resolution (Mitchell, 2011). Traditional pollen analysis uses sediments from large lakes or bogs which collect pollen from a radius of tens

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of kilometres. The pollen from numerous vegetation communities is mixed before deposition and so identifying dynamics in a single community is restricted by uncertainties. Surface sample measurements, and modelling studies have shown, however, that the pollen records contained within small hollows in forests are dominated by pollen from a more local source area within a 100 m radius (Sugita, 1994). Small hollow pollen analysis from forested sites thus provides data on forest dynamics at the forest stand scale (Bradshaw, 2007; Overballe-Petersen and Bradshaw, 2011). Such data that are chronologically controlled can be likened to the analysis of vegetation patterns in forest stand quadrats through time. The pollen data derived from such investigations is, however, a proxy for vegetation. Differences in production, dispersal and preservation of pollen across species is an important issue (Seppä, 2007). In addition, pollen is most consistently identified to genus rather than species level, and occasionally only to family level, so the taxonomic resolution of pollen data do not match that of quadrat data from vegetation surveys. Recent advances in modelling pollen dispersal at landscape and local scales (Sugita, 2007a,b) provides an approach for deriving vegetation compositional data for woodland communities from small hollow pollen data (e.g. Nielsen and Odgaard, 2010; Sugita et al., 2010; Overballe-Petersen et al., 2013) but the empirical data on pollen dispersal for the relevant taxa required to drive these models in Atlantic oakwoods are not yet available. Consequently it is necessary to rely on pollen data as the vegetation proxy for this investigation. Despite these restrictions, pollen do provide proxy data of vegetation change over millennial timescales that can be analysed to address compositional change in forested communities (Birks, 2007).

In this paper changes in the biodiversity of Atlantic oakwoods are quantified over millennial timescales from a series of sites located along the west coast of Ireland. This permits the investigation of the research question: how has human exploitation of Atlantic forests impacted on their biodiversity and what is the long-term legacy of this exploitation?

2. Methods

Pollen records were selected from small hollows in Irish Atlantic oakwoods that had independent dating and covered at least the last 3000 years. This resulted in the selection of 4 pollen records (Table 1). Further details on the sites and generation of the pollen records can be found in the original publications (Table 1).

The combined dataset for the four sites is represented by 101 pollen samples and a total of 93 different pollen taxa. Chronologies were developed for each site using the original radiocarbon dates run through the Bayesian modelling technique Bchron (version 3.1.4 using the IntCal09 calibration curve) which uses a stochastic linear interpolation process (Haslett and Parnell, 2008). From this process it was possible to derive a date for each pollen sample (Supplementary material).

Ordination of the pollen data using non-metric multidimensional scaling (NMS) in PC-ORD 6.08 (McCune and Mefford, 2011) was used to explore the relationship between pollen samples. The taxon richness of each pollen sample can be derived from the number of pollen taxa identified but since the number of pollen grains identified varies across samples it is necessary to rarefy the taxon richness to a constant pollen sum for each site (Birks and Line, 1992). Rarefaction of the data was computed with the rarefaction function within the vegan package (Oksanen et al., 2012) in R (R Core Team, 2012) to derive an alpha diversity measure for each sample (RareN). RareN was thus scaled to the lowest pollen count from the samples within a site. The rate of change (ROC) between adjacent pollen samples was quantified by the squared chord distance (Grimm and Jacobson, 1992). The chronologies were then used to scale ROC to units per 100 years. The surface pollen sample for each site was assumed to represent present day conditions. The Sørensen (Bray–Curtis) distance in NMS ordination space for each site was used as a measure of change (beta diversity) in older samples compared to the present day. To facilitate presentation and further analysis, the derived RareN, ROC and beta diversity metrics were pooled across the four sites and averaged for each 1000 year period. In addition to the pollen data, microscopic charcoal data derived from the pollen slides are also available from each site (see original publications for details). The site chronologies were used to derive the charcoal accumulation rate (CHAR) for each sample and these data were also averaged for each 1000 year period. Differences among 1000 year periods were tested for using the non-parametric Kruskall Wallis test followed by post hoc Mann–Whitney *U* tests with Sidak's adjustment for multiple tests.

The degree of biodiversity heterogeny between, and within, the 1000 year periods was assessed through Multi-Response Permutation Procedures (MRPP) in PC-ORD 6.08 (McCune and Mefford, 2011). The Sørensen (Bray–Curtis) distance measure was used on the pollen data sets. MRPP derives a test statistic, T, with its associated p-value which indicates the separation between time periods (more negative values represent stronger separation). MRPP also calculates the chance-corrected within-time period agreement statistic, A, to measure the effect of sample size. $A = 0$ if the average within-time period distance is equal to that expected by chance, $A > 0$ if average within-time period distance is less than that expected by chance (McCune and Mefford, 2011).

3. Results

Summary pollen data from the shortest record (Uragh Wood) and the NMS ordination of the full data set are reproduced here to provide an illustration of one of the data sets (Fig. 1). The pollen diagram illustrates how the site was initially dominated by *Pinus* but this tree declined about 2000 years ago. High charcoal levels in recent centuries are associated with the reduction in tree cover. A successional recovery of the canopy is evident following the reduction in charcoal levels (Fig. 1a). The NMS ordination recommended a 2-dimensional solution with a final stress of 10.92 and a final instability < 0.00001. The trajectory that the vegetation community takes over the last 3200 years is depicted by vectors joining the pollen samples in ordination space (Fig. 1b). This

Table 1
Small hollow pollen records from Irish Atlantic oakwoods, listed in order from south to north.

Site name	Grid reference	Altitude (m)	Length of record (years)	Source reference
Uragh	09°41′49″W 51°48′27″N	70	3200	(Little et al., 1996)
Derrycunihy	09°35′53″W 51°58′27″N	40	6900	(Mitchell, 1988)
Camillan	09°31′56″W 52°01′04″N	20	6800	(Mitchell, 1988)
Brackloon	09°33′17″W 53°45′31″N	85	5900	(Little et al., 2001)