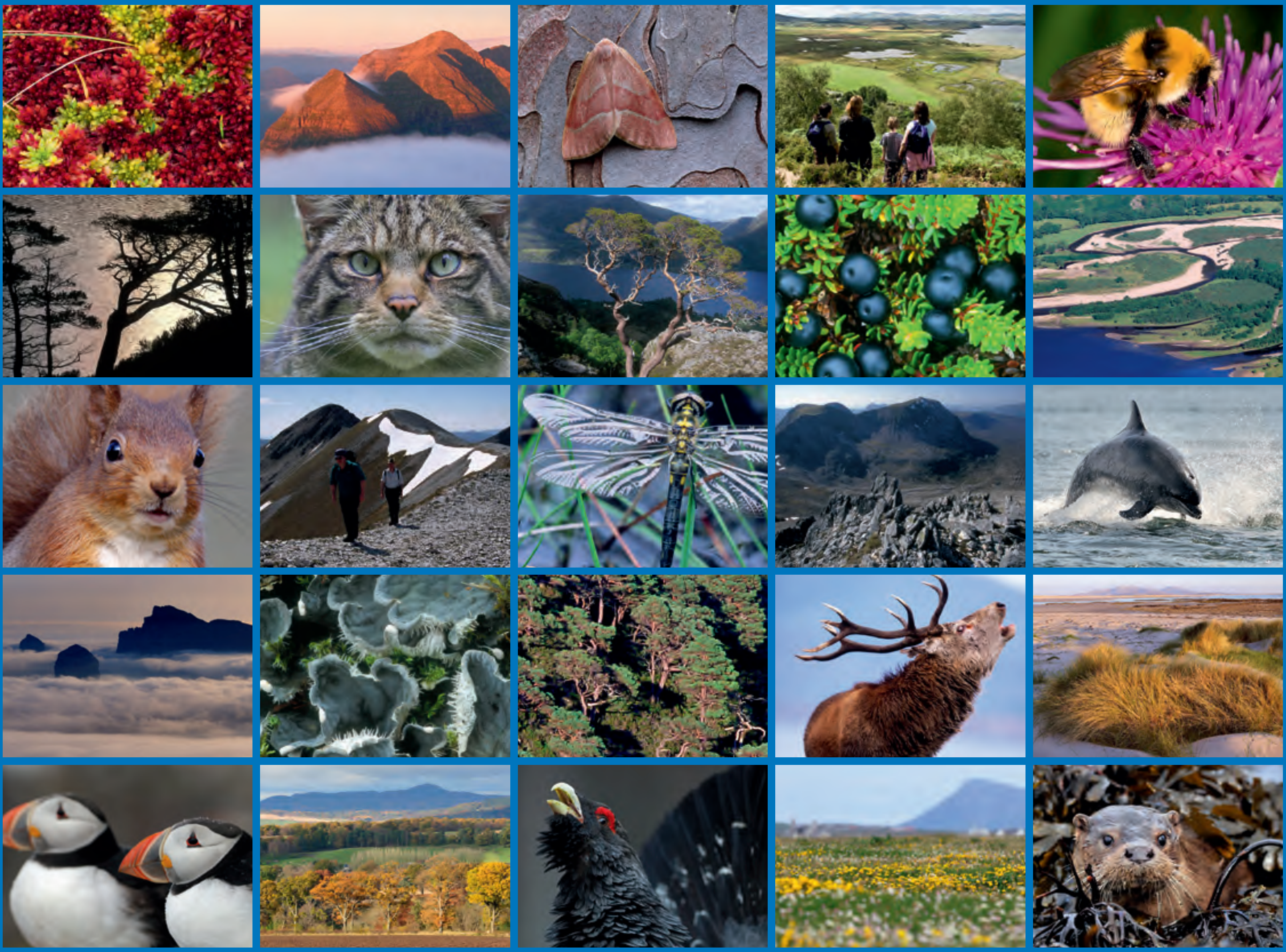
Scottish Natural Heritage
Commissioned Report No. 426

Lichen epiphyte dynamics in Scottish Atlantic oakwoods – The effect of tree age and historical continuity



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COMMISSIONED REPORT

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Lichen epiphyte dynamics in Scottish Atlantic oakwoods – The effect of tree age and historical continuity

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COMMISSIONED REPORT

Summary

Lichen epiphyte diversity in Scottish Atlantic oakwoods – The effect of tree age and historical continuity

Commissioned Report No. 426 (iBids project no. 1406)
Contractor: Royal Botanic Garden Edinburgh (Dr Christopher Ellis)
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Background

Scottish Atlantic oakwoods are a conservation priority, not least because of their characteristic epiphyte communities, which are representative of cool-temperate rainforest. Forests with a strong representation of temperate rainforest epiphytes are globally disjunct; Scotland provides probably the best examples of these epiphyte communities in Europe, owing to the long ecological continuity of forest remnants, and low levels of air pollution. However, Scotland's extant oakwood habitat is fragmentary, in a human-modified cultural landscape. There is a move towards the regeneration of Scottish native woodlands – including Atlantic oakwoooods. This report summarises research to quantify the temporal processes which control the development of oakwood epiphyte communities – enabling ecological information on epiphytes to inform strategies in forest regeneration.

The research strategy adopted sampling at two scales: individual trees of different age, occurring in sites with different levels of historic continuity, i.e. *Recent* sites (regenerated since *c.* 1860) and *Ancient* sites (assumed continuously present since the mid-18th Century, and possibly for millennia). Two response variables were quantified: species composition, and species richness, including the richness of conservation priority and indicator species. Previously published research had demonstrated shifts in epiphyte composition and richness controlled by tree age, and for forest sites with contrasting continuity: our cross-scale approach was expected to provide a template, from which the temporal pattern of epiphyte community development might be quantified with respect to tree age and site continuity.

Main findings

- We found that oak demographic structure was remarkably similar comparing *Recent* with *Ancient* sites.

- Accordingly, it is possible that the oak trees sampled from the *Ancient* sites were sampled from areas that had been clear-cut, and that this break in continuity was undetected using cartographic reconstructuction. However, Coppins & Coppins (2002) WSIEC indicator species were significantly more abundant in our samples from *Ancient* than *Recent* sites, pointing to a source-sink effect, i.e. colonisation from *Ancient* to adjacent *Recent* sites. This favours an interpretation in which there is **long-term** continuity of stands within

Ancient sites (over-lapping generations of oak trees across coupes within oak coppice) – even if the sampled oak tree ages are similar in age.

- On this basis, we found no effect of site historic continuity on the epiphyte composition or richness **of sampled oak trees**, either in terms of community-level patterns, or in a search across individual species.

- We attribute this negative result, **first** to the effect of historic management in the 19th Century (coppice) on the structure of oakwoods (an absence of old (> 200 yr) and degenerating trees), combined with a recent lack of intensive management and regeneration: thus, oak demography was similar compared between ostensibly *Recent* and *Ancient* sites.

- **Second**, our results show that for an equivalent micro-habitat type (oaks of a similar age), there is no evidence for an accumulation of species richness as a function of site continuity: an equivalent micro-habitat is not more species rich in an *Ancient* than in a *Recent* site.

- Our findings emphasise an essential difference between 'historic continuity' (the time over which a site has been wooded), and old-growth structure. Sites with long historic continuity (e.g. AWI Class 1a sites) may – considering oak trees – be functionally equivalent to recently regenerated sites. They lack old-growth structural attributes which significantly alter broad compositional patterns.

- We present evidence that spatial proximity between *Recent* and *Ancient* sites is important in controlling epiphyte community structure. On the basis of this evidence, targeted regeneration around a spectrum of sites with contrasting species composition can be expected to help increase the resilience of Scotland's rainforest epiphyte communities.

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Acknowledgements

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1 INTRODUCTION

The west-coast of Scotland matches the bioclimatic conditions for 'cool-temperate rainforest', a habitat-type which is restricted to disjunct and extremely localised regions of the terrestrial biosphere (Fig. 1A & B). Where native semi-natural forest occurs within this climate zone it is a European conservation priority (e.g. the oceanic facies of the EU Annex 1 habitat 91A0, '*old sessile oakwood*').

Many of Europe's forests which formerly occupied an Atlantic-oceanic climatic zone have been destroyed or degraded (Hannah *et al*., 1995; see also Fig. 3.15, Millennium Ecosystem Assessment, 2005), and remnant examples may have lost their characteristic epiphyte flora as a consequence of pollution impacts (Hawksworth & Rose, 1970; Van Herk *et al*., 2003). Scotland retains areas of remnant forest with long historical continuity (Walker & Kirby, 1989; Roberts *et al*., 1992), in a clean-air environment (NEGTAP, 2001), and in an oceanic climate (Fig. 1B); woodland habitats along Scotland's Atlantic coastline therefore provide internationally-important examples of European cool-temperate rainforest and their epiphyte communities.

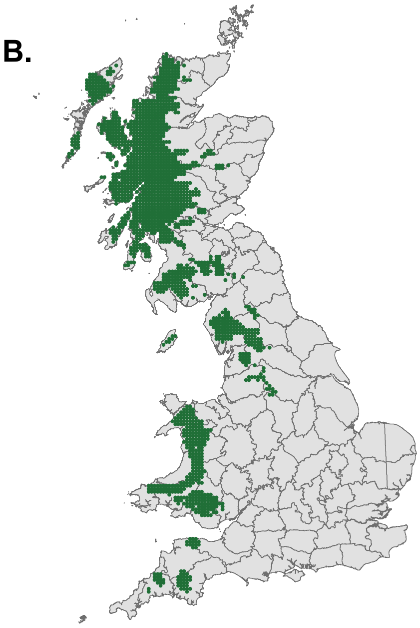

Figure 1. A. The global distribution of temperate rainforest (Rhind, 2003); B. The distribution of cool-temperate rainforest bioclimate in Britain, as defined by Alaback (1991): annual precipitation > 1400mm, with 10% of annual precipitation during summer, and a mean July isotherm < 16 °C.

Despite their ecological and conservation importance, Scotland's remnant Atlantic-oceanic woodlands are fragmentary and exist as isolated elements in a human-modified cultural landscape. Palaeoecological evidence suggests that prior to widespread human modification of the post-glacial forest (5000-2500 BP), the west-coast of Scotland was occupied by a forest mosaic, though characterised by the extensive presence of *Quercus* spp, with *Corylus avellana* (Birks, 1988; Tipping 2003).

Oak remains an important tree in woodlands along the Scottish west-coast (e.g. NVC W11, *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland: Rodwell, 1991), and 'Atlantic oakwood' is a habitat-type of immense natural and cultural importance (Hall & Stone, 2005). Existing Atlantic oakwoods have undergone structural change as a consequence of human management of the woodland resource, e.g. selective management for timber, tannin and charcoal (Smout, 2005; Smout *et al*., 2007). Nevertheless, certain remnant Atlantic oakwoods have retained a long-period of woodland cover, and present-day woodlands may occur on sites that have been continuously wooded since post-glacial colonisation: so-called 'ancient woodlands' (Rackham 2006; Smout *et al*., 2007).

Given the conservation importance of Atlantic oakwood, its cultural significance, and, combined with a commitment to regenerate native Scottish woodland (Hampson & Peterken, 1998; Forestry Commission, 2000), there is an imperative to examine the propensity of restoring Atlantic oakwood into new sites (Moseley *et al*., 2005). This report examines the potential of not simply regenerating the trees, but also the epiphytes which characterise cool-temperate rainforest (Fig. 2).

*Figure 2. Elements of the '*Lobarion*' epiphyte community (*Lobaria pulmonaria *and Lobaria* scrobiculata*) – examples of large foliose lichens which characterise epiphyte communities in cool-temperate rainforests.*

1.1 Epiphytes

Cool-temperate rainforest is strongly characterised by the composition, diversity and biomass of its lichen epiphyte flora (*cf*. Goward & Spribille, 2005; Affeld *et al*., 2008). Oakwoods occur widely across Europe (Rodwell, 2005), but it is the functional comparison of Scotland's Atlantic oakwood epiphytes – with those of cool-temperate rainforests elsewhere – that defines this habitat as uniquely important in Britain. Most notably, this biogeographic similarity includes the dominant presence of large foliose lichens which are associated with a cyanobacterial symbiont (Green & Lange, 1991; McCune, 1993; Affeld *et al*., 2008).

The lichen epiphytes associated with Atlantic oakwoods can be classified into three categories:

- *Geographically Restricted*. These species occur in woodland habitats only in hyper-oceanic climates. Examples include species such as *Pseudocyphellaria crocata* (Fig. 3). The distribution of these species appears to be obligately oceanic. It is unlikely that species within this category were ever common during the Holocene outside an oceanic bioclimate.

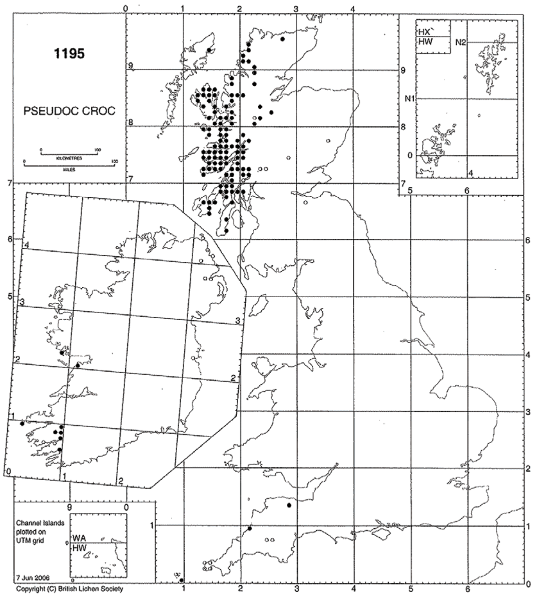

Figure 3. The British distribution of Pseudocyphellaria crocata*, an example of an oceanic specialist. Compare this dot-map to the extent of Britain's cool-temperate rainforest bioclimate in Fig. 2 (above). Map courtesy of the British Lichen Society mapping scheme (Prof. M.R.D. Seaward, University of Bradford).*

- *Geographically Preferred*. This category includes species which are commonest within Scotland's hyper-oceanic climate, but which may have occurred across a wider climatic range during the Holocene. Examples include *Lobaria pulmonaria*: western Scotland has some of the largest European populations of this species, though it is believed to have been widely distributed throughout Europe during a period when old-growth forest was more extensive (e.g. Rose, 1988). Its current distribution is thought to be a consequence of relaxed habitat specificity in an optimum climate (Ellis & Coppins, 2007a; Ellis *et al.*, 2009).

Oakwoods provide important habitat structure for species within these two categories, though the lichen epiphytes may not be facultatively associated with oak trees themselves, and may occur preferentially on companion trees within oakwoods, e.g. rowan (*Sorbus aucuparia*), or hazel (*Corylus avellana*).

Species for which oak is the major phorophyte tree species provide the third category:

- *Oakwood Species*. Approximately 15 lichen epiphyte species are recorded predominantly from oak, and from Atlantic oakwoods (Coppins & Coppins, 2005).

1.2 Study Aims

The broad aim of this study was to provide information on the response of oceanic lichen epiphyte communities – those characteristic of cool-temperate rainforest – to the spatial and temporal dynamics of Scotland's Atlantic oakwoods. It was intended that this information on epiphyte response would be used to inform woodland regeneration strategies and biodiversity conservation.

The study was subject to four management guidelines:

1. The study was carried out over an 18 month period, and is therefore limited to an examination of epiphyte communities on oak trees themselves.

2. The study focused on two variables of interest to the conservationist: **species composition** (the types of species present), and **species richness** (the number of species present).

3. The study examined trends in these response variables at two scales: among **individual trees**, and among **individual sites**.

4. To document and explain temporal trends in epiphyte communities (succession) – which might be used to inform long-term management strategy – the study compared species composition and richness to the effects of tree age, and site historical continuity, in addition to a range of alternative explanatory variables.

The guidelines for the study were established at draft stage with SNH (Jeanette Hall) and with respect to a specific requirement: assuming epiphyte communities respond to tree age, and stand continuity, the epiphyte response will be used to establish a minimum requirement for forest regeneration. Rephrased, *it will be possible to know how long it takes not only to regenerate trees, but to regenerate epiphyte communities, both in terms of tree planting, and the longer-term effects of site-scale continuity*.

1.2.1 Questions/Hypotheses

Focussing on the two spatial-temporal scales (tree and site) and epiphyte response variables (composition and richness), the study is able to test the following questions/hypotheses:

1. Are general patterns in species composition fundamentally different among oak trees in *Ancient* and *Recent* woodland stands, e.g. is the '*Lobarion*' is restricted to *Ancient* sites?

2. More specifically, are certain species (rather than entire communities) restricted to oaks in *Ancient* sites?

3. Does species composition change predictably as an oak tree ages, i.e. do certain species only occur on older trees?

4. Is oak tree species richness higher for *Ancient* than for *Recent* sites: e.g. for a tree of a given age, species richness may be higher within an *Ancient* compared to a *Recent* site?

5. Is the occurrence of conservation priority species skewed towards *Ancient* as opposed to *Recent* sites?

2 METHODS

2.1 Site Selection

Prior to site selection, two continuity classes were defined:

- *Ancient*. These sites were drawn from the Ancient Woodland Inventory's Class 1a polygons (Walker & Kirby, 1989; Roberts *et al.*, 1992). They are assumed to be continuously wooded since 1750, with a high probability of continuous woodland cover since post-glacial forestation.

- *Recent*. These sites were drawn from AWI Class 3 polygons (Walker & Kirby, 1989; Roberts *et al.*, 1992). They are shown as clear of woodland or isolated tree symbols on 1st Edition 6 inch-to-the-mile OS maps. They are assumed to have been planted or naturally colonised with trees in the period since 1860-70.

Twelve sites were selected for survey, comprising six of each antiquity class. Sites were paired, so that each *Recent* site was matched with a nearby *Ancient* site.

The limiting factor in selecting sites was locating sites of *Recent* antiquity that were directly verifiable on the original maps and contained sufficient numbers of oak trees to be sampled (all Class 3 sites were re-verified for this study). For this reason, the *Recent* sites were selected first, with *Ancient* sites selected on the basis of proximity to their *Recent* paired site. As much as possible, paired *Ancient* sites were also matched in terms of aspect, altitude and soil type (Fig. 4).

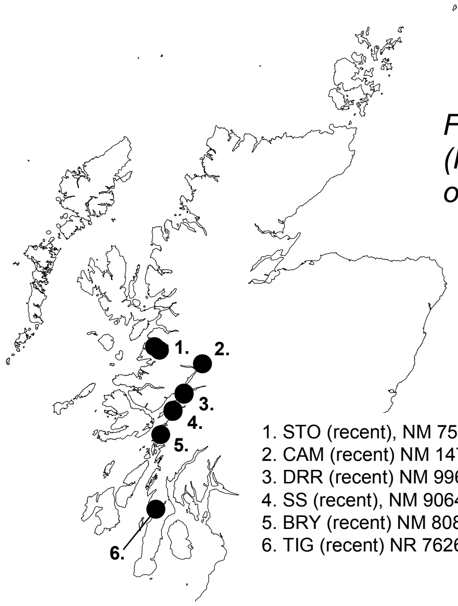

Figure 4. The position of paired study sites (Recent and Ancient *woodlands) along Scotland's oceanic Atlantic coastline (cf. Fig. 2)*

1. STO (recent), NM 758943; STB (ancient) NM 797916
2. CAM (recent) NM 147800; CCU (ancient) NN 149802
3. DRR (recent) NM 996560; STA (ancient) NM 995557
4. SS (recent), NM 906418; AS (ancient) NM 907420
5. BRY (recent) NM 808220; BNC (ancient) 808224
6. TIG (recent) NR 762610; SOI (ancient) NR639610

2.2 Tree Selection

For each selected site, ten sample points were placed randomly within the site boundary, prior to fieldwork, using ArcView GIS (ESRI, 2005). The sample points were used as the basis for tree selection. Selection of trees was stratified by size, aiming to ensure a representative age range was sampled. Two size classes were used: small trees defined as < 20 cm dbh and medium trees ≥ 20 cm dbh. (A third size class – large – defined as larger than 100 cm dbh was dropped as no trees of this size were ever found).

During fieldwork the sample points were located with GPS. Beginning at each sample point, the closest oak tree of a given size class was chosen as a sample unit. Locating medium-sized trees (≥ 20cm dbh) was generally straightforward, but small trees (< 20cm dbh) were often rare or locally distributed. If a search of five minutes did not yield a suitable tree then the selection was deferred, and the first suitable tree encountered in the course of travel between sample points was substituted.

2.3 Tree Sampling

A range of attributes were sampled from selected trees (below); for trees with multiple stems, the largest stem was selected as the sampling unit.

- *Spatial coordinates*. The GPS unit was positioned immediately adjacent to the tree, to record position by averaging location data over the course of 200-500 seconds.

- *Girth at Breast Height* (gbh). The girth of the tree was measured at breast height (1.3m above ground) with a girthing tape; later converted to diameter at breast height (dbh). Standard forestry conventions for measuring dbh were used (Mackie & Matthews, 2006).

- *Lichen species*. All lichen species were recorded on the stem from ground level to 2m height. Those species not identifiable in the field with the use of a hand-lens and spot-test chemicals were collected: a small sample was removed with a knife and placed into a labelled packet. Abundance of each species was estimated as area cover, according to five cover-class codes (Table 1). A minimum search effort of 15 minutes was spent inspecting each stem.

Table 1. Cover codes for epiphyte abundance.

	Cover Range
Cover Code	
1	< 10 cm^2
2	10-110 cm^2
3	100-1000 cm^2
4	0.1-1 m^2
5	> 1 m^2

- *Other epiphytes*. Common or abundant bryophyte and vascular epiphytes were recorded with the lichen species.

- *Ground vegetation*. A time limited survey was made of the ground vegetation within a 2m radius of the tree base (≤ 3 minutes). Species with greater than approximately 40 % cover were recorded as ‘dominants’.

- *Tree age*. An increment borer was used to take a core from each sampled tree. The core samples were stored in labelled tubes. The cores were collected from breast height (1.3m) to coincide with the girth measurement. In cases where the core could not be collected from this point on the stem, it was sampled lower down, and a separate record of stem girth at the point of core extraction was recorded.

- *Photograph*. A digital photograph was taken for each tree, to aid future relocation. Images are stored on a secure server at RBGE.

2.4 Herbarium Analysis

Difficult species returned to RBGE were identified using standard light microscopy at low (x10 – x50) and high power (x100 – x1000), coupled with herbarium resources (accessioned specimens) and chemical tests including UV fluorescence, paraphenylenediamine (Pd) and thin layer chromatography where necessary (Orange *et al*., 2001). Nomenclature for lichens follows Smith *et al*. (2009), and for vascular plants, Stace (1997).

Trees were aged using dendrochronology. Tree cores were mounted into a wooden block, and were sectioned using a razor-blade. The section was examined under low power (x10 – x50) and seasonal rings counted. Where a tree core did not include the heart wood, the number of missing rings was estimated by alignment with a series of nested concentric circles, whose differential radius matched the average width of the innermost 5 tree rings.

2.5 Statistical Analysis

Statistical analyses were targeted towards specific questions, which together answered the broad project aims (see 1.2, *Study Aims*, above). Technical summaries are provided here for completeness, though it is not necessary to follow the detail of the Methods in order to understand the Results (Section 3).

In all cases we restricted our analysis to taxa which had been positively identified, thereby avoiding potential duplication in species counts.

2.5.1 Are there fundamental differences in oak populations compared among Recent and Ancient sites?

To answer this question we tested: (i) for trends in growth rate, as well as (ii) the demographic structure of the oak populations among sites (i.e. the proportion of younger and older trees contributing to a population).

2.5.1.1 Growth-rate

To test for a relationship between tree size (dbh) and age (yr), we used a generalised linear mixed model (GLMM, with Maximum Likelihood estimation (ML)) to compare tree age and stand age (fixed effects) to dbh (response), with site identity as a random effect. A full model included the interaction between tree age and historical continuity (allowing for variable growth rates between sites with different continuity). We first normalised variance in the random component of the full model using a fixed variance structure (Zuur *et al*. 2009): this normalised plotted residuals and minimised values for Akaike's information criterion. Second, we simplified the fixed effects using log-likelihood tests to perform stepwise comparisons (Crawley 2007; Zuur *et al*., 2009), and we plotted the optimum fitted model.

Analysis was performed in R (2008), using the 'lme' function in the package 'nlme' (Pinheiro & Bates, 2000; Venables & Ripley, 2002).

2.5.1.2 Oak Demography

We compared the age-structure of tree populations among *Recent* and *Ancient* sites, and among paired sites (i.e. sets of adjacent *Recent* and *Ancient* sites). We used re-sampling with replacement (bootstrapping, N = 10,000), to generate robust estimates of median and standard error (bootstrap s.d.) for tree-ages at intervals corresponding to the minimum, lower quartile (25th percentile), median, upper quartile (75th percentile), and maximum of the oak population structure (Crawley, 2007; Maindonald & Braun, 2010).

We generated Q-Q plots for paired sites, and tested for population differences between *Recent* and *Ancient* sites, using a Mann-Whitney test (W) to compare tree-age at equivalent intervals, and using a Wilcoxin signed rank test (W_r) to restrict the comparison to between the paired *Recent* and *Ancient* sites (thereby allowing for potential regional variation in demographic structure). We repeated these comparisons using equivalent parametric tests (*t*-tests and paired *t*-tests).

Analysis was performed in R (2008), using the 'boot' package and function for resampling (Canty, 2002), and the base-package for nonparametric and parametric *t*-tests.

2.5.2 Do Ecological Indicator Species provide evidence for differences in site continuity?

We tested for differences in the richness and abundance of previously established West of Scotland Indicator Species for Ecological Continuity (Coppins & Coppins, 2002), using a Mann-Whitney test to compare among *Recent* and *Ancient* sites. We refer to these as WSIEC indicators.

2.5.3 Is epiphyte composition different, compared between Ancient and recently regenerated (Recent) woodland?

Focussing on lichens (excluding lichenicolous fungi), we examined patterns in species composition, comparing: (i) variation between *Recent* and *Ancient* sites, with (ii) variation among each of the paired sites (i.e. adjacent *Recent* and *Ancient* sites).

This allowed us to examine the extent to which species composition is controlled by historical continuity of woodland cover, or, alternatively, by spatial proximity. We used four complementary methods: a multi-response permutation procedure (MRPP); ordination by detrended correspondence analysis (DCA); hierarchical cluster analysis (HCA); and Mantel tests (Mt).

We examined three response-types.

First, analysing community composition for species abundances on individual trees (MRPP and DCA) we tested whether community composition – including variation among individual trees within a site – scales-up to generate between site trends.

Second, we calculated the median abundance for a species, across trees with non-zero values within a site, thereby controlling for variation between individual trees. We asked whether there were general differences in species abundances among sites (MRPP, HCA), and tested these differences with respect to spatial proximity (Mt).

Third, we aimed to discount the effect of patchiness in species abundances within a given site (between trees), and used the maximum occurrence of a species on any tree within a site. This measure may be more informative than median values across many sampled trees (MRPP & HCA & Mt, as above).

2.5.3.1 Multi-response Permutation Procedure

To implement MRPP we first calculated a pair-wise distance matrix using the Sørenson distance coefficient, with rank-transformation (McCune & Grace, 2002). MRPP then proceeds by calculating the weighted-mean within-group distance (δ), and comparing this to a Pearson type III distribution using the test statistic *T*, to describe the separation between groups: where *T* = the difference between the observed and expected δ, divided by the standard deviation of the expected δ. MRPP also describes an effect size (*A*), providing a chance-corrected within-group agreement: i.e. testing for no difference in average within-group ranked distances (McCune & Grace, 2002)

MRPP was implemented using PC-Ord v. 4.41 (McCune & Mefford, 1999).

2.5.3.2 Detrended Correspondence Analysis

We implemented ordination by DCA, with down-weighting of rare species, to examine compositional variation among trees and across all sites. Our use of DCA (as opposed to linear-response tools, e.g. PCA) was confirmed by the gradient length for axis one of 4.107 (cf. Lepš & Šmilauer, 2003). We tested for differences in DCA axis scores among *Recent* and *Ancient* sites and among sets of paired sites, using a Mann-Whitney test (*W*), and Kruskal-Wallis test (*H*), respectively.

DCA was implemented in CANOCO v. 4.5 (ter Braak & Šmilauer, 2002), with comparisons of axis scores implemented using the base-package in R (2008).

Having derived a summary of variation in epiphyte composition among trees, we compared DCA axes to: (i) evidence for systematic contrasts between epiphyte communities, and (ii) changes in the ground-layer vegetation explaining differences in local soil conditions.

First, we calculated for each tree the cover of sampled epiphytes which had been assigned into contrasting community-types by James *et al*. (1977), focussing on seven different communities: (i) Cladonion coniocraeae, (ii) Graphidion scriptae (excluding the sub-group Pertusarietum amarae), (iii) Lecanorion subfuscae, (iv) Lobarion pulmonariae, (v) Parmelion laevigatae, (vi) Parmelion perlatae, and (vii) Usneion barbatae. To provide a proportional measure, the observed cover value was divided by the theoretical maximum possible cover (where all species within a community would have a cover class of 5, see Table 1). We calculated the correlation of community types with DCA axes, and, where significant, plotted epiphyte community variation as vectors onto an ordination diagram.

Second, we calculated Ellenberg Indicator Values based on the vascular plant ground flora (presence-absence of species), for light, and soil moisture, pH and nitrogen (Hill *et al*., 1999). We calculated the correlation of Ellenberg scores with DCA axes, and, where significant, plotted the proxy values for local environmental condition as vectors onto an ordination diagram.

2.5.3.3 Hierarchical Cluster Analysis

We implemented hierarchical cluster analysis (McCune & Grace, 2002) using the Sørenson distance coefficient, and with tree joining by flexible beta linkage ($\beta = -0.25$). Dendrograms clustering sites by epiphyte community similarity were implemented for the median and maximum abundances of species present at a site.

Hierarchical cluster analysis was implemented using PC-Ord v. 4.41 (McCune & Mefford, 1999).

2.5.3.4 Mantel Tests

We used Mantel tests to compare community dissimilarity to the spatial distance between sites. Community dissimilarity was measured using the Sørenson distance coefficient. Spatial proximity was compared to epiphyte community dissimilarity among sites ($n = 12$), and among sets of paired sites ($n = 6$), using median species abundance values.

Mantel tests were implemented using 100,000 permutations, in the DOS program ZT (Bonnet & van der Peer, 2002).

2.5.4 *What is the relative importance of tree age in controlling epiphyte species composition?*

We examined in detail the factors controlling community composition within sites, while discounting between-site differences. We used canonical correspondence analysis (CCA), to directly compare the ordination of epiphyte communities to selected environmental factors: tree age, tree size (dbh), and Ellenberg scores for light, and soil moisture, pH and nitrogen (Hill *et al*., 1999). CCA was implemented with stand identity as a dummy covariable.

We used a permutation test (9999 randomisations) to forward select environmental variables significantly explaining community composition, and estimated the relative importance of these as the variation explained by canonical axes, compared to total inertia (cf. Lepš & Šmilauer, 2003).

CCA was implemented in CANOCO v. 4.5 (ter Braak & Šmilauer, 2002).

2.5.4.1 Functional Trait Analysis

We performed an extended analysis of the CCA results, to examine whether there are successional trends in epiphyte communities. If so, these should be evidenced by predictable and non-random patterns in species traits, with respect to oak tree age. Thus, we used the bi-plot rule in CCA (Lepš & Šmilauer, 2003), projecting sample scores perpendicularly onto the CCA vector for tree age. This provides an alignment of epiphyte communities with respect to tree age, though partitioning out any unique site effects (i.e. stand identity as a dummy covariable, see above) while also accounting for the combined effect of other important environmental factors selected into the CCA using a Monte Carlo test (see above).

We used the position of epiphyte communities along a CCA gradient describing age-conditioned community structure, to explain abundance values for contrasting trait groups in terms of growth-form and reproductive strategy: (i) fruticose lichens (asexual, including *Evernia prunastri*), (ii) *Cladonia* spp, (iii) sexual foliose macrolichens, (iv) asexual foliose macrolichens, (v) sexual microlichens, (vi) asexual microlichens (excluding Leprose species), (vii) Leprose species (*Lepraria* and *Chrysothrix* spp), and extending the analysis to include (viii) bryophytes.

For the species assigned into the six trait-groups, we summed the cover classes per sampled tree; to provide a proportional measure, the observed cover value was divided by the theoretical maximum possible cover (where all species within a trait-group would have a cover class of 5, see Table 1). Trait groups were compared to the age-community gradient using generalised additive models (GAMs), with analysis in R (2008) using the ‘gam’ function in the package ‘mgcv’ (Wood, 2006). GAMs were implemented using a Poisson variance-structure, and with smoothing functions held within 2 degrees of freedom.

2.5.5 *Are certain species consistently associated with old trees and/or Ancient sites?*

In Section 2.5.4 we searched for general differences in composition among oaks in *Recent* and *Ancient* sites. Here, we search for specific species which may be restricted to oaks in *Ancient* sites, or may be restricted to old oak trees.

We used Indicator Species Analysis (Dufrêne & Legendre 1997) to test for significant associations between individual species (ISA-species), and sites with contrasting historical continuity. For site data we used species median abundances, and maximum abundances (see Section 2.5.2, above). Indicator Species Analysis compares the proportional abundances and frequencies of a species within a target group (e.g. *Ancient* sites) relative to the abundance/frequency across all groups, yielding an indicator value (McCune & Grace, 2002). We tested the significance of each species' indicator value using a Monte Carlo permutation test, with 10,000 randomisations.

We repeated Indicator Species Analysis, to test for associations between epiphyte species and older trees (≥ 150 yr) occurring in *Ancient* sites.

2.5.6 Do tree age, tree size and/or stand-scale ecological continuity explain tree-scale patterns in species richness?

First, we compared the species richness for trees within a site, among sites with different historical continuity. We used a Mann-Whitney test (W) to compare tree-scale richness among *Recent* and *Ancient* sites.

Second we compared site-scale species richness for selected epiphyte groups, based on species conservation assessment criteria (Woods & Coppins, 2011).

Third, we tested for a relationship between the richness of lichen epiphyte species on a tree (response), and explanatory variables (tree size (dbh), tree age (yr) and site historical continuity), using a generalised linear mixed model (GLMM, with Maximum Likelihood estimation (ML)), with site identity as a random effect. A full model included the interaction between tree scale variables (tree size and age) and historical continuity. Residuals were normally distributed without a requirement to alter the variance structure (Zuur *et al*. 2009). We simplified the fixed effects using log-likelihood tests to perform stepwise comparisons (Crawley 2007; Zuur *et al*. 2009), and we plotted the optimum fitted model.
Analysis was performed in R (2008), using the 'lme' function in the package 'nlme' (Pinheiro & Bates 2000; Venables & Ripley, 2002).

2.5.7 Is total site richness explained by environmental heterogeneity, historical continuity, and/or landscape connectivity?

We compared the lichen epiphyte species richness of oak trees at a site, to stand and landscape parameters: local environmental heterogeneity, historical continuity, or connectivity with adjacent old-growth woodland.

First, because different sites were subject to different sampling effort (number of trees sampled), we needed to derive a robust estimate of site-scale species richness. We used EstimateS v. 8.2.0 (Colwell, 2006) to generate estimates of site-scale richness using seven different nonparametric metrics for incidence-based data (Magurran, 2004): Chao2, Jack-knife1 and Jack-knife2, ICE, bootstrap, MM1 (Michaelis-Menten richness estimators averaged over randomizations (mean among runs)), MM2 (Michaelis-Menten richness estimators computed once for Mao Tau species accumulation curves).

The least intensively sampled site comprised 10 trees (n = 10). Therefore, for sites where n = 18 and n = 20, we compared the difference between the estimated richness value for the complete sample set (all sampled trees at a site), and a reduced sample set where n = 10. We then selected the richness estimator which provided the smallest mean difference, i.e. the most consistent estimates compared between different within-site sample sizes, and we used this metric to provide our site-scale estimates of total richness.

We summarised environmental heterogeneity using the explanatory variables forward selected into CCA analysis (see Section 2.5.3, above). We used principal components analysis with data standardised and centred (cf. Lepš & Šmilauer, 2003), to calculate the distance between trees in environmental space. We then estimated heterogeneity for a site, by calculating the average pair-wise distance in ordination space, between trees within sites, using Pythagoras' theorem.

We calculated landscape connectivity to ‘Ancient’ woodland, using Arcview GIS (ESRI, 2005): i.e. the extent of AWI Class 1 and 2a woodland surrounding a study site, within four consecutively sized buffers, at 1km, 5km, 10km and 25km.

Residuals were normally distributed, and we used multiple linear regression with AIC stepwise selection to optimise the fit of explanatory variables to site-scale species richness. Analysis was performed using the base package in R (2008).

3 RESULTS

We positively identified a combined total of 198 lichens and lichenicolous fungi (173 lichens, and 25 lichenicolous fungi), from 192 sampled trees across twelve sites (Appendix 1).

3.1 Oak woodland demographic structure

The youngest sampled tree had an estimated age of *c*. 15 yr, and the oldest *c*. 188 yr. Approximately 47 % of sampled trees were > 100 yr, and *c*. 10 % were > 150 yr. The raw data age structure of sampled oaks is shown in Fig. 5; significant over-lap in the age structure of *Recent* and *Ancient* sites is immediately apparent.

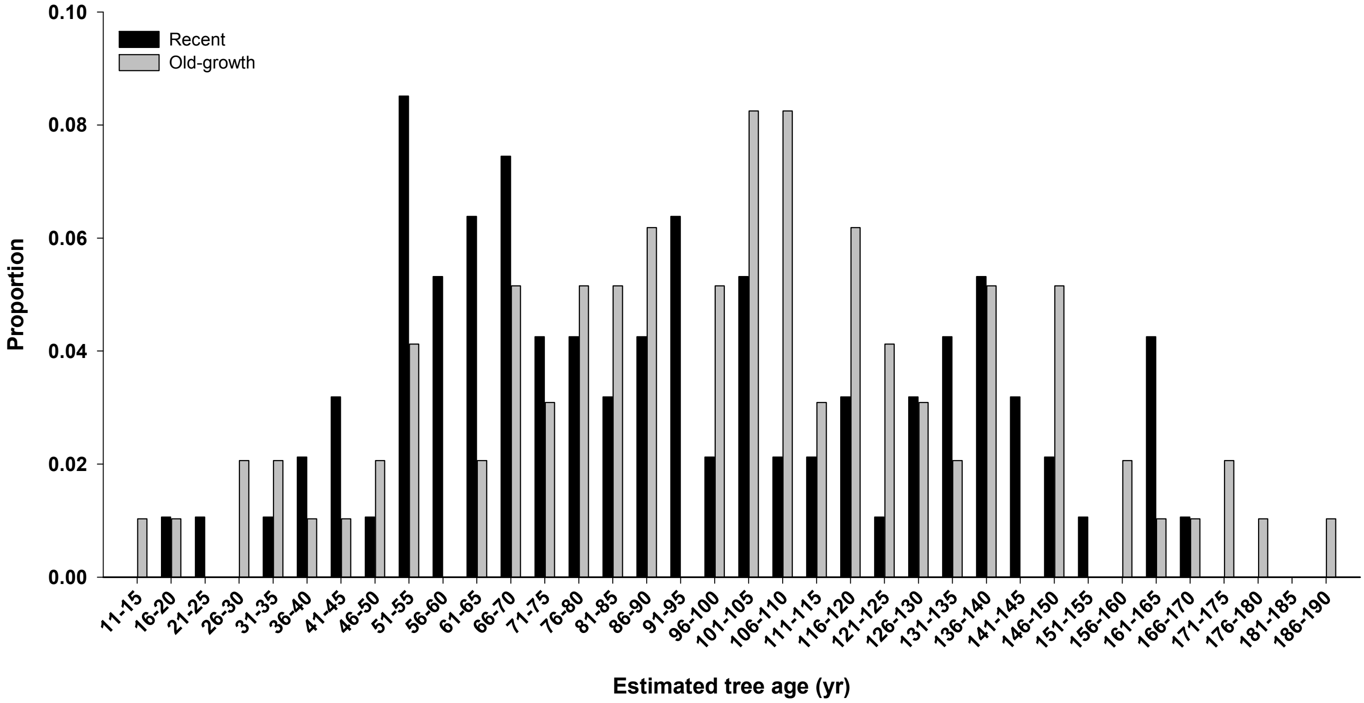

Figure 5. Histogram to show the general raw data age structure of oak trees, for pooled Recent *and* Ancient *sites.*

3.1.1 Growth-rate

The relationship between tree size (dbh), and estimated tree age and stand age, was best described using a GLMM (site as a random effect), and dropping both the interaction term (L = 2.05, df = 1, P = 0.1519) and stand age from the fixed effects model structure (L = 0.18, df = 1, P = 0.6711), while retaining tree age (L = 96.12, df = 1, P < 0.0001). This suggests that growth rates (size-age relationship) did not significantly differ among *Recent* and *Ancient* sites: thus, we fitted a single population model to the data (Fig. 6).

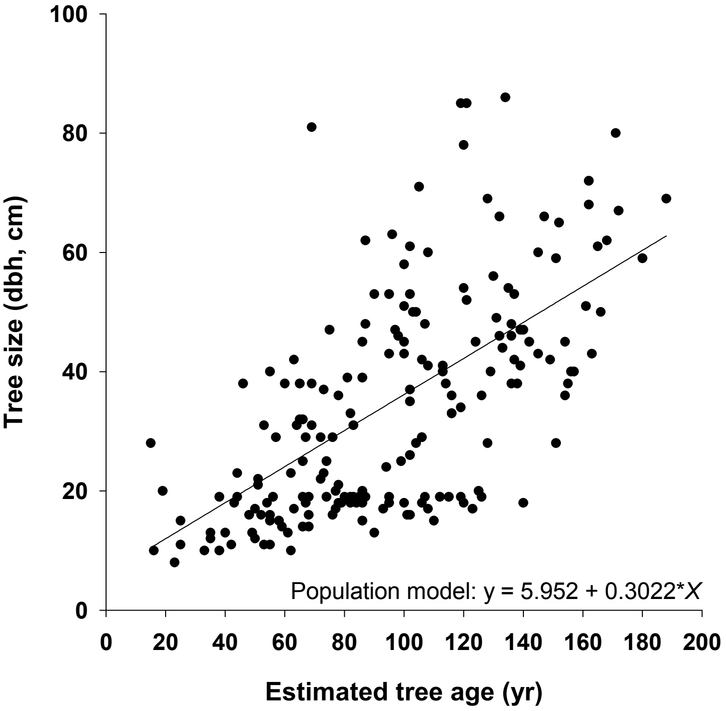

Figure 6. The relationship between tree age (yr), estimated by dendrochronology, and tree size (dbh): GLMM coefficients were statistically significant (intercept, P = 0.0499; age, P < 0.0001, both with 178 df); estimated s.d. for random effects (intercept) = 5.953.

3.1.2 Oak Demography

Using bootstrap resampling to test the age structure of oak populations (Table 2; Fig. 7), we found no significant difference between the demography of oak trees among sites with different continuity (*Recent* and *Ancient*); this was true even when we allowed for possible regional trends in population structure by accounting for paired *Recent* and *Ancient* sites (Table 2). Comparisons were confirmed non-significant when analysed using equivalent parametric tests: *t*-tests and paired *t*-tests (not reported).

Table 2. Results for a non-parametric Mann-Whitney test, to compare bootstrap estimates for tree ages – among Recent *and* Ancient *sites – at different intervals within the oak population: minimum, lower quartile, median, upper quartile and maximum ages. The test was repeated using a Wilcoxin signed rank test, to compare values between paired* Recent *and* Ancient *sites.*

Percentile (age structure)	Mann-Whitney	Test statistic Wilcoxin signed rank
Min	U = 13.5, $P = 0.5211$	$Wr = 17.5$, $P = 0.1718$
25th	U = 17, $P = 0.9372$	$Wr = 9$, $P = 0.8438$
Median	U = 19, $P = 0.9372$	$Wr = 8$, $P = 0.6875$
75th	U = 20, $P = 0.8182$	$Wr = 7$, $P = 0.5625$
Max	U = 19, $P = 0.936$	$Wr = 6$, $P = 0.4004$

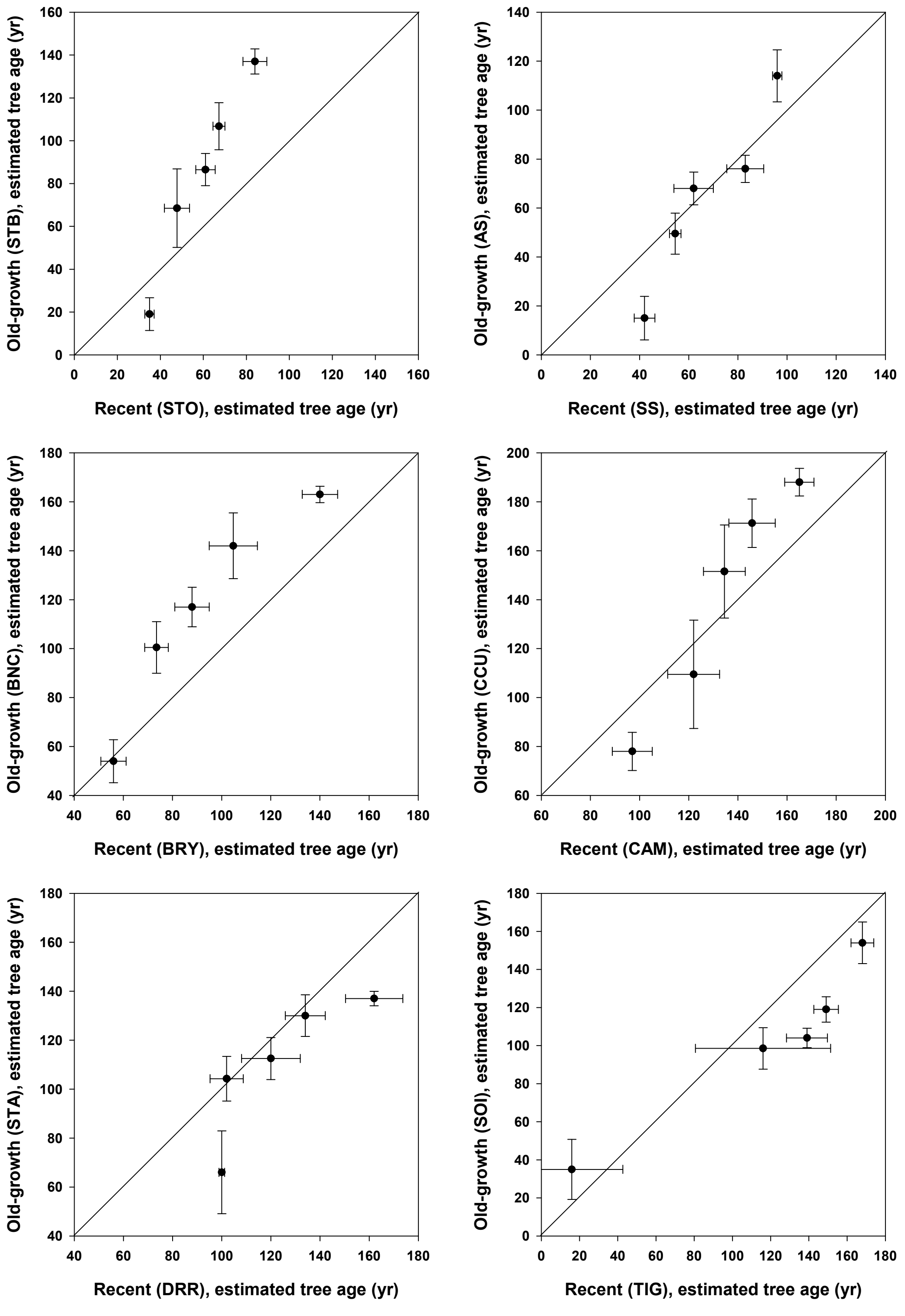

Figure 7. Plots to compare bootstrap estimates of the median, at age intervals from oak populations among paired Recent *and* Ancient *sites: minimum, lower quartile, median, upper quartile and maximum ages, with bootstrap standard deviations (error bars). Points below the solid line indicate an older estimated age at a given population interval for the* Recent *sites, points above the line indicate an older age for the* Ancient *sites. There is no evidence that oak populations tend to have a different age structure compared between sites with different historical continuity.*

3.2 Do Ecological Indicator Species provide evidence for differences in site continuity?

We examined previously established Indicators of Ecological Continuity for the West Coast of Scotland: i.e. WSIEC indicators (Coppins & Coppins, 2002). We sampled twenty WSIEC Indicators across all stands, with no difference in their richness among the *Recent* and *Ancient* sites: $W = 13$, $P = 0.4665$. However, there was a significant difference in the abundance of WSIEC indicators ($W = 13$, $P = 0.03006$), with evidence for their greater abundance in *Ancient* sites.

3.3 Is epiphyte composition different, compared between *Ancient* and recently regenerated (*Recent*) woodland?

Using rank-transformed MRPP to compare community composition between *Recent* and *Ancient* sites, and among sets of paired sites (i.e. comparing between adjacent pairs of *Recent* and *Ancient* sites), the balance of evidence is strongly in favour of spatial proximity controlling patterns of species composition, and not historical continuity (Table 3).

T-values and effect size (*A*) are greater for the comparison among sets of paired sites, than for the comparison between *Recent* and *Ancient* sites: i.e. at the tree-scale *P*-values for the comparison among *Recent* and *Ancient* sites are much weaker with relatively small effect size.

At the site-scale *P*-values for the comparison among *Recent* and *Ancient* sites are non-significant.

Table 3. Results of MRPP to test for significant differences in community structure, comparing between Recent *and* Ancient *sites, and comparing among the paired sites.*
*MRPP cannot analyse groups containing only two entities.

Scale of analysis	MRPP comparison: Between Recent and Ancient	MRPP comparison: Among Paired sites
Tree-scale: abundance	$T = -3.198$	$T = -49.818$
	$P = 0.0083$	$P < 0.000001$
	A = 0.0114	A = 0.401
Site-scale: median abundance	$T = 1.483$	N/A*
	$P = 0.957$	
	A = -0.0744	
Site-scale: maximum abundance	$T = 1.383$	N/A*
	$P = 0.947$	
	A = -0.0718	

Ordination by DCA provided additional strong evidence for the more important role of spatial proximity in structuring communities, compared to historical continuity of woodland cover.

DCA ordination explained 9.9% of variation along axis one, and 4.9% of variation along axis two, which we consider to be a reasonable summary given a large dataset (33,216 data points). The importance of spatial proximity is therefore confirmed by DCA ordination, which – based on epiphyte composition – clearly identifies trees from contrasting locations (Fig. 8).

This is demonstrated statistically, with axis one values weakly significant compared between *Recent* and *Ancient* sites (W = 3845, P = 0.0482), and very strongly significant for comparison among sets of paired sites (H = 109.66, P < 0.000001). Similarly, DCA axis two values were not significantly different compared between *Recent* and *Ancient* sites (W = 5079, P = 0.2191, and very strongly significant for comparison among paired sites (H = 85.4, P < 0.000001).

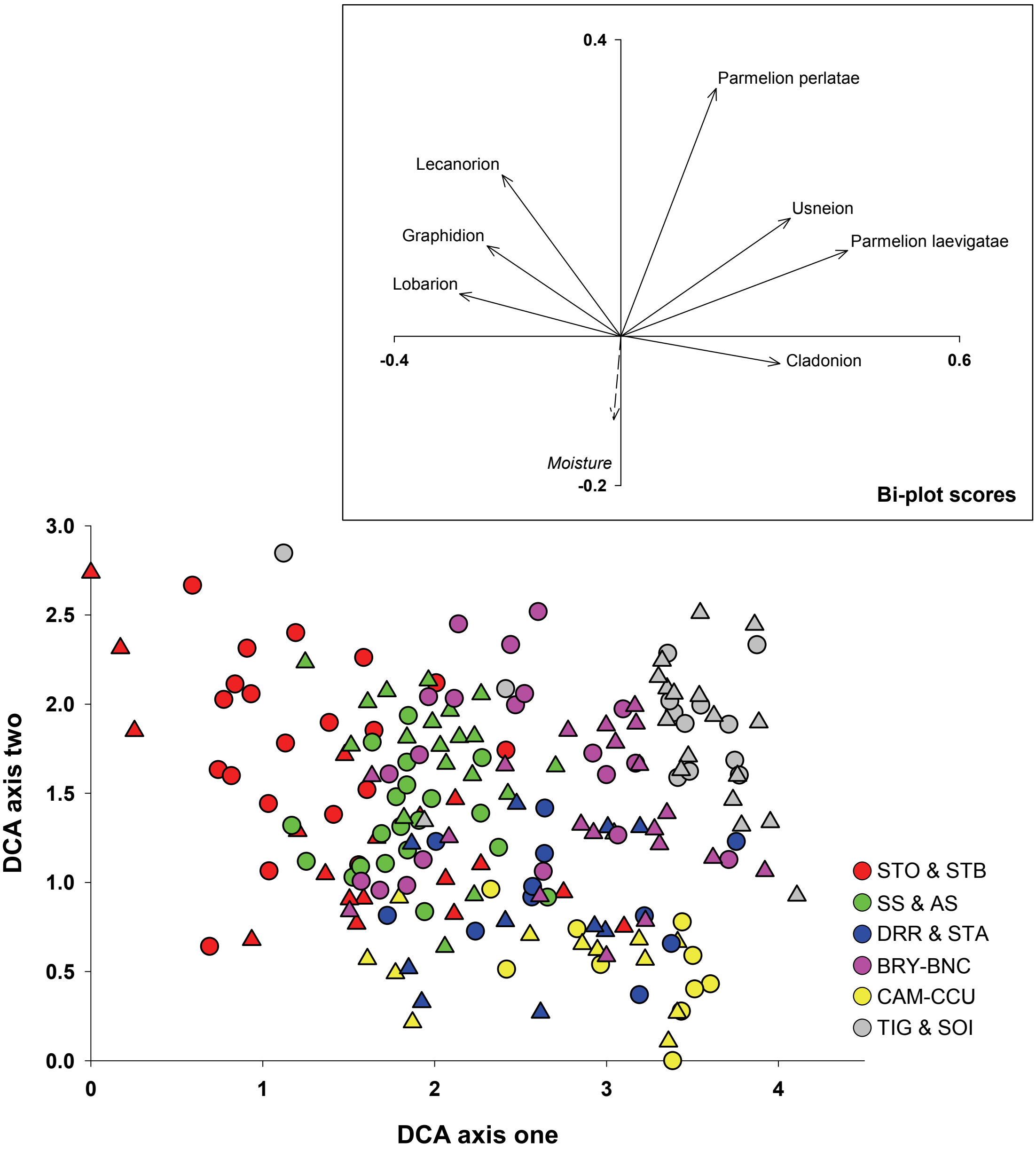

Figure 8. Ordination plot based on detrended correspondence analysis (DCA): notice that trees tend to cluster according to colour (spatially proximate paired sites), rather than by symbols which indicate historical continuity (● = Recent *sites,* ▲ = Ancient *sites). Where significantly correlated with axis sample scores, joint bi-plot scores are shown (inset, above) for epiphyte communities (James* et al.*, 1977) and Ellenberg factors (Hill* et al.*, 1999).*

Comparing lichen epiphyte communities among all sites thus indicated that species turnover – variation in species composition – is more likely to be explained by spatial proximity, than it is by historical continuity compared among closely associated sites. Likewise, hierarchical clustering consistently grouped together the paired sites, based on their similarity in epiphyte composition, and did not discriminate community-groupings for sites with equivalent historical continuity (Fig. 9).

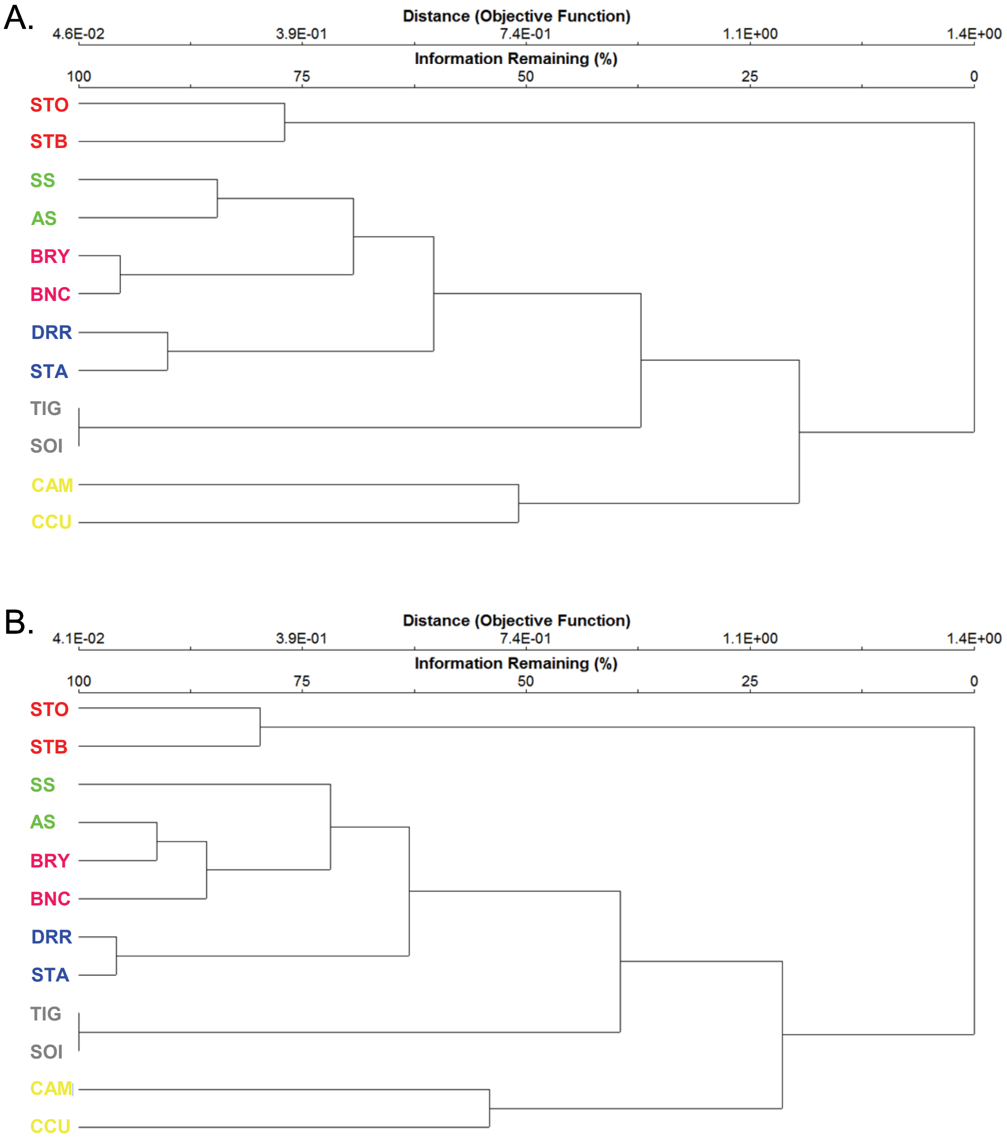

Figure 9. Hierarchical dendrograms, to compare lichen epiphyte species composition among sites: A. using species median abundance values, B. using species maximum abundance. In both cases, spatially proximate paired-sites tend to be grouped together, with no evidence for grouping based on historical continuity.

The strong evidence for epiphyte community similarity based on spatial distance is supported when using Mantel tests to correlate among all twelve sites, i.e. including comparison between paired sites which are spatially very close: r = 0.524, P = 0.00067. However, applied at a different spatial-scale, with correlation among the six sets of paired sites, there was no evidence for epiphyte community similarity based on spatial distance: r = 0.248, P = 0.267.

3.4 Does tree age control epiphyte species composition?

We used site identity as a covariable in CCA, to partition out the unique differences among sites, or sets of paired sites, in terms of species composition (see Figs 8 & 9, above). Monte Carlo permutation selected tree age as the most important of our variables controlling species composition, though also including Ellenberg values for soil N, soil moisture, and light, as well as tree dbh (Table 4). CCA axes one and two captured 38.3 % and 27.4 % of the species-environment relationship, respectively.

*Table 4. The results of ordination by CCA, comparing the community composition for trees with site identity partitioned out, and identifying putative explanatory variables using forward selection with Monte Carlo permutation (*P *values derived using 9999 permutations).*

CCA diagnostics		
Explanatory variables	F, *P*	% variation explained
Tree age	F = 4.53, *P* = 0.0001	6.54 %
Soil N	F = 2.75, *P* = 0.0001	
Soil moisture	F = 2.81, P = 0.0001	
Light	F = 1.94, *P* = 0.0004	
Tree size	F = 1.61, P = 0.0057	

Using the CCA defined age-community gradient as a framework, significant models were fitted for all eight trait-groups using GAMs. Although the age-community gradient is a statistically significant explanatory variable for all trait-groups, model quality in terms of deviance explained is variable, and ranges between *c*. 2 % for fruticose and sexually-reproducing foliose lichens, and *c*. 13 % for asexual microlichens (Fig. 10). The models nevertheless point to consistent trends in trait-groups which might be generalised: 1. Sexual crustose lichens decrease along a community gradient on ageing trees, 2. Bryophytes and leprose lichens increase along this gradient, and 3. Asexually-reproducing microlichens, foliose macrolichens and *Cladonia* spp peak at mid tree ages (Fig. 10).

3.5 Are certain species consistently associated with old trees and/or *Ancient* sites?

In addition to broad-scale trends in species composition, it is possible that certain epiphyte species (a sub-set of the entire community) may be restricted to *Ancient* sites, and/or old oak trees. We used Indicator Species analysis to test for the occurrence of individual species which may be associated with *Ancient* sites. Given the compositional differences between sets of paired sites (see Section 3.2, above), the identification of robust indicator species is expected to be problematic: i.e. indicator species must operate across a range of contrasting epiphyte community-types. Testing for oak tree indicator species for *Ancient* sites, we found no evidence of significant indicators, based on the median species abundance (*P* values from 0.1518 to 1, mean = 0.8547), or the maximum species abundance (*P* values from 0.1178 to 1, mean = 0.8545). Restricting this analysis to species associated with older oak trees (≥ 150 yr) in *Ancient* sites, there were six significant indicators (Table 5).

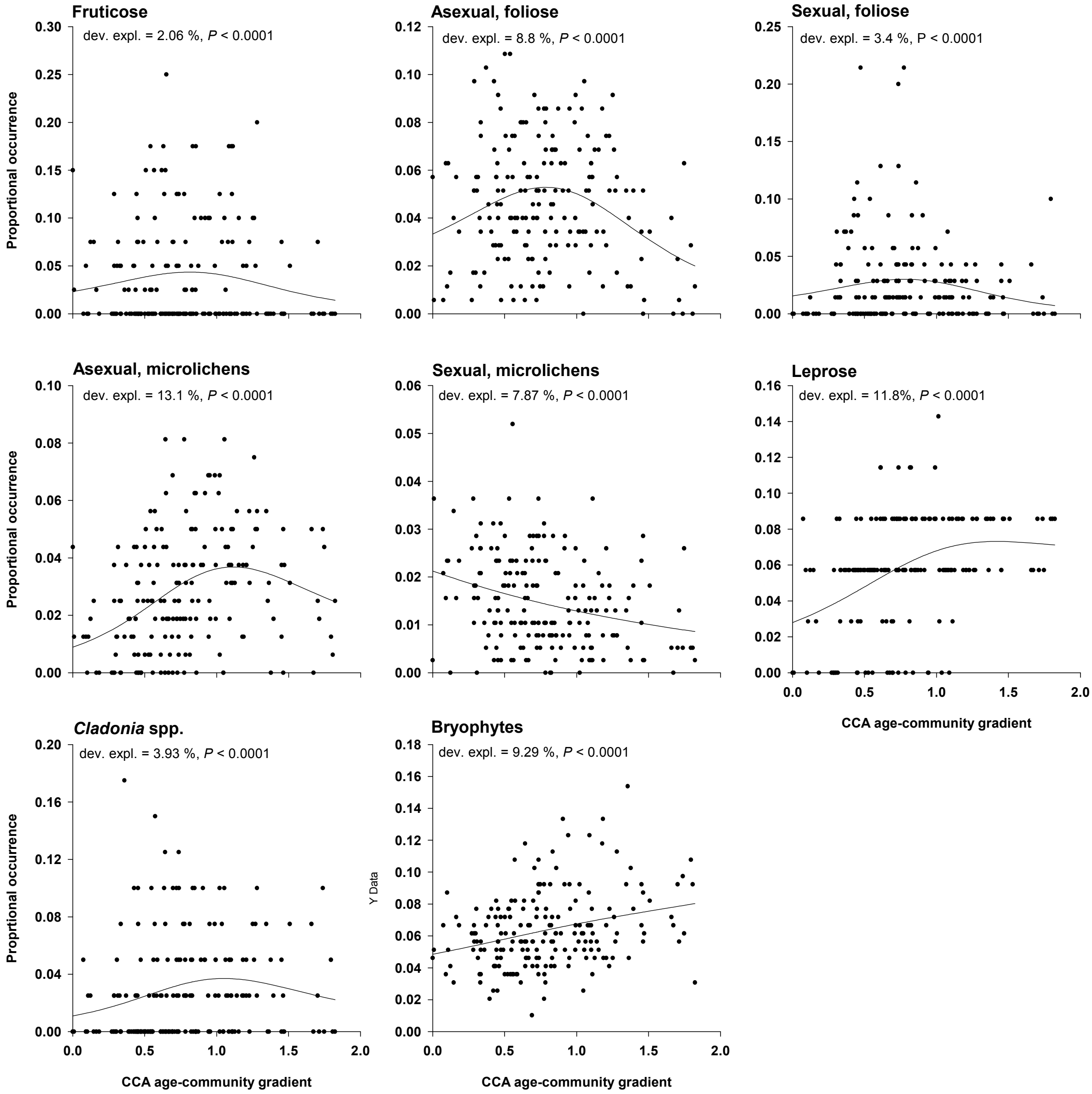

Figure 10. Generalised additive models, showing the response of contrasting epiphyte trait-groups to the tree age-epiphyte community gradient derived using CCA bi-plot scores.

Table 5. Significant indicator species associate with the oldest trees (≥ 150 yr) in Ancient *sites.*

Epiphyte Species	Indicator species *P*-value
Biatora vernalis	0.0306
Lecanactis abietina	0.0258
Lepraria lobificans	0.0112
Opegrapha multipuncta	0.0306
Peltigera hymenina	0.0306
Trapeliopsis pseudogranulosa	0.0039

3.6 Do tree age, tree size and/or site historical continuity explain patterns in species richness?

Values of epiphyte species richness recorded for individual oak trees were not significantly different among *Recent* and *Ancient* sites: *W* = 4373, *P* = 0.5449 (Fig. 11).

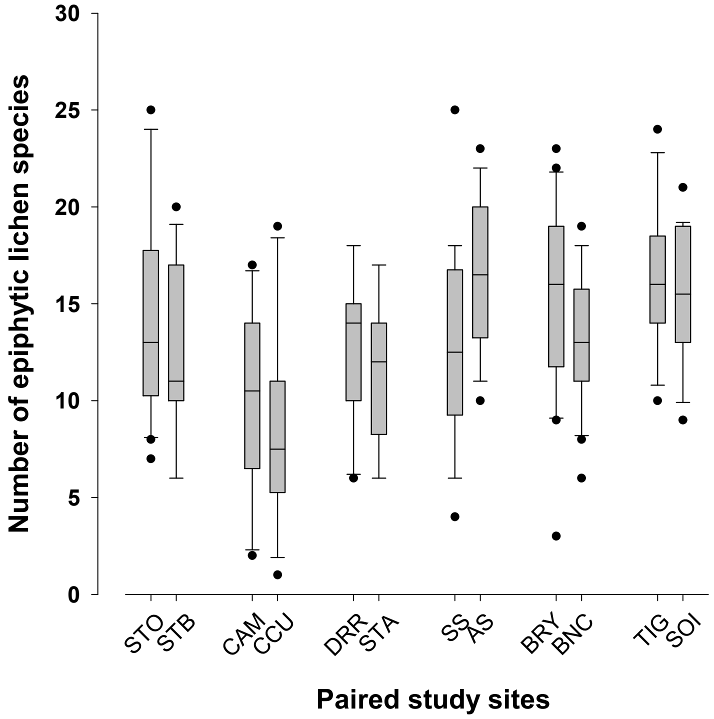

Figure 11. Box-plots comparing the species richness of individual trees, sampled from paired Recent *and* Ancient *sites (cf. Fig. 4).*

In addition to total species richness, we tested for differences in the number of species occurring in *Recent* and *Ancient* sites that are considered rare and of conservation interest (Nationally Scarce, or Nationally Rare according to Woods & Coppins, 2011).

We found 33 species that were Nationally Scarce or Nationally Rare – there was no difference in the numbers of these species among *Recent* and *Ancient* sites: *W* = 12, *P* = 0.3708. This observation extends to include the occurrence of the IUCN 'near threatened' *Leptogium brebissonii* in two Recent stands (STO and SS). When we considered the proportional occurrence of species, there was no significant difference for the abundance of Nationally Scarce or Rare species (*W* = 19, *P* = 0.9372).

The relationship between species richness, and tree-age and dbh, and historical continuity, was best described using a GLMM (site as a random effect), and dropping, during stepwise tests: (i) the interaction between tree-age and ecological continuity (*L* = 0.342, *df* = 1, *P* = 0.5588), (ii) the interaction between tree-dbh and ecological continuity (*L* = 0.546, *df* = 1, *P* = 0.4599), and (iii) the effect of ecological continuity (*L* = 0.517, *df* = 1, *P* = 0.4721), while retaining (iv) the interaction between tree-age and tree dbh (*L* = 13.163, *df* = 1, *P* = 0.0003), in addition to the effects of tree-age and tree dbh.

In order to examine the effect of tree-age and dbh on species richness, we plotted the optimum model, using five tree-sizes: at the median, 10th, 25th, 75th and 90th percentiles observed across all sites. We combined these tree sizes with age values that occurred within the 95% confidence intervals of the tree size – age relationship (Fig. 12).

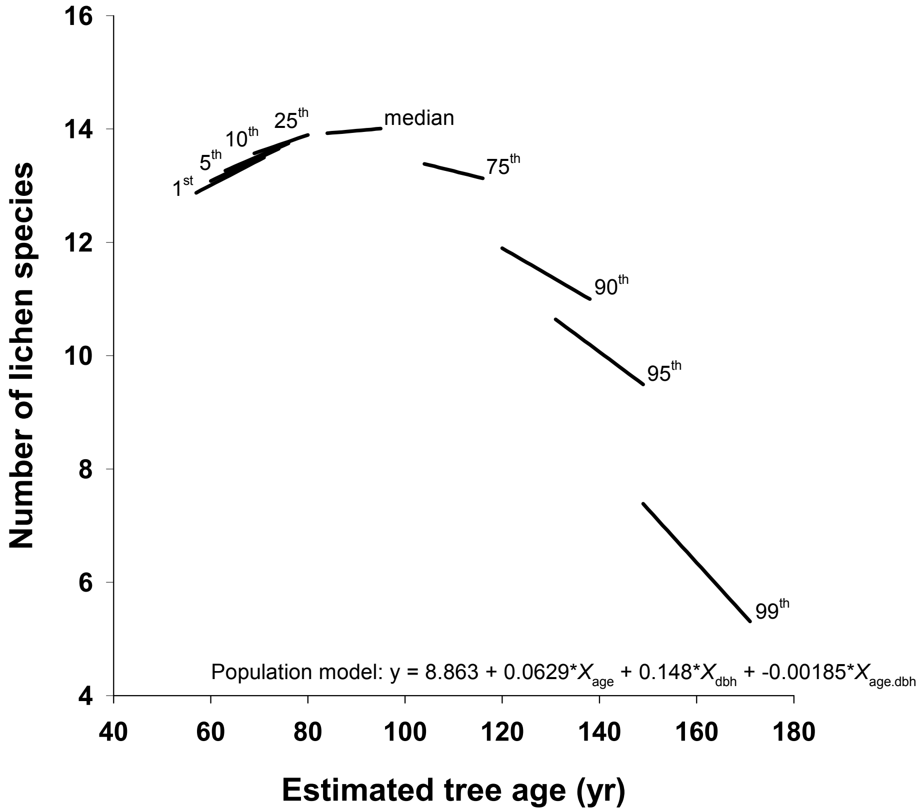

*Figure 12. The modelled response of species richness to estimated tree age, and corresponding tree sizes: 1st percentile (10 cm dbh), 5th percentile (12 cm dbh), 10th percentile (14 cm dbh), 25th percentile (18 cm dbh), median (30 cm dbh), 75th percentile (45.5 cm dbh), 90th percentile (61 cm dbh), 95th percentile (68.5 cm dbh) and 99th percentile (85 cm dbh). GLMM coefficients were statistically significant (intercept, $P < 0.0001$; age, $P = 0.0013$, dbh, $P = 0.0032$, age*dbh, $P = 0.0004$, each with 177 df); estimated s.d. for random effects (intercept) = 1.922.*

The model coefficients and plotted response indicate that species richness increases with tree age and tree size when each acts independently, but, owing to a significant interaction between age and size, species richness declines on older and larger trees.

3.7 Is total site richness explained by extent, environmental heterogeneity, historical continuity, or landscape connectivity?

First, we compared the shift in estimated richness, for a scenario with 10 sampled trees, and with 18 or 20 sampled trees. Our aim was to select the most stable estimator of total oak tree richness, across different sample sizes. On this basis, the metric MM1 (Michaelis-Menten richness averaged over randomizations (mean among runs)), provided the smallest shift in estimated richness for different sample sizes, and was selected as our estimator (Fig. 13).

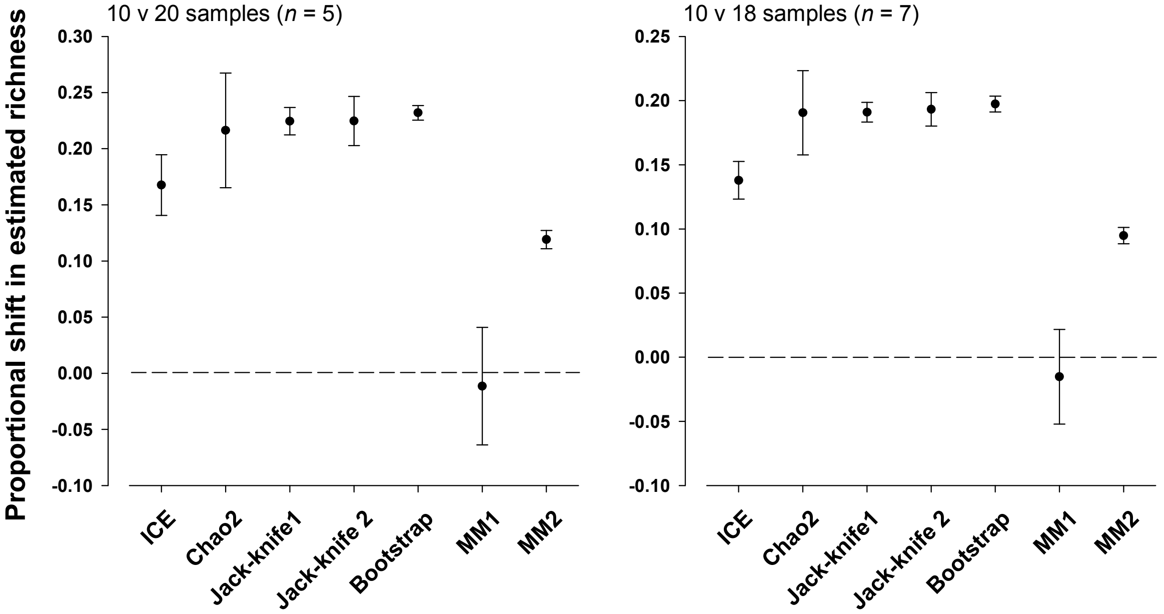

Figure 13. The shift in estimated richness, for different metrics, compared for different sample sizes: comparing n = 10, to n =18 and n = 20, respectively.

We compared estimated total oak tree richness to stand heterogeneity, historical continuity and landscape connectivity. PCA was used to estimate stand heterogeneity, with the first three PCA axes explaining > 80% of environmental variation (axis one = 37.8%, axis two = 27.6% and axis three = 16.3%). We therefore extended Pythagoras' theorem to calculate the distance between points in 3-dimensional space, and used the average pair-wise distance calculated for trees sampled from a site, as a measure of within-site heterogeneity.

Model optimisation (multiple regression without interaction) selected landscape connectivity at a 10km scale as the single factor explaining site-scale species richness, though this was not significant: $R^2 = 0.162$, $P = 0.19$ with 10 df. Dropping other connectivity measures from the full model (1km, 5km and 25km), and allowing 10km connectivity to interact with historical continuity and environmental heterogeneity, a second optimised model included the interaction between 10km connectivity and heterogeneity. This second model had a marginally improved AIC (113.28, 112.81), but was not significant: $R^2 = 0.422$, $P = 0.2$ with 8 df.

4 DISCUSSION

4.1 A Model System for Analysis

It was our aim at the beginning of this study to provide detailed information on the development of Atlantic oakwood epiphyte communities, with respect to tree age and site continuity. To do this we sampled trees of contrasting age, from paired sites which were either of *Recent* origin (regenerated since 1860), or of *Ancient* origin (ostensibly continuously wooded since the mid-18th Century, and probably for millennia). Based on a consensus in previously published evidence, we expected this to provide a template for measuring epiphyte community dynamics at two scales: the tree-scale, and the site-scale.

4.2 The Weak Effect of Continuity on Richness and Indicator Species

In contrast to initial expectations, we found no effect of supposed historical continuity on species richness at a tree- or a site-scale, or a preference among individual species (i.e. ISA-indicators). This might be explained by three woodland history scenarios, with alternative consequences for the interpretation of our results.

- *Scenario 1*: *Ancient* sites have been clear-felled.
  No difference in epiphytes compared between *Ancient* and *Recent* sites might be explained if our *Ancient* sites had in fact been clear-felled at some point in the recent past – e.g. the late 19th Century – possibly explaining the consistency in tree age values.

- *Scenario 2*. Selective tree management.
  An alternative possibility might consider our sampled *Ancient* woodlands to be cultural as well as natural landscape features, having been subject to a long-history of selective human management, and substantial modification of tree demography compared to 'old-growth' forest (Smout, 2005; Smout *et al*., 2007). Consequently, by examining lichens on the oaks themselves (the managed woodland resource), our study is comparing *Ancient* sites with sequential tree regeneration which – despite over-lapping generations of trees among coupes – has led to the normalisation of oak demography among *Ancient* and *Recent* sites.

- *Scenario 3*. Sampling bias.
  Finally, because we focussed on oak trees - it must also be considered that the *Ancient* sites examined may retain some alternative structural characteristics of old-growth that were not detected: e.g. a wider diversity of companion tree species, or dead wood.

These three scenarios have different implications.

In the first scenario (clear-felling), it is easy to explain consistent patterns in species richness among *Recent* and *Ancient* sites, which are effectively equivalent. It also explains why we did not detect any ISA-indicators compared among *Ancient* and *Recent* sites – however, the clear-felling scenario brings into question the utility of established WSIEC indicators, a spectrum of which have been detected across all 12 sites (mean number of species = 5.5, maximum = 10), despite a remarkably low sampling effort, i.e. the lower boles of 10-20 randomly selected trees per woodland.

Scenarios two and three present more complex alternatives.

4.2.1 Species richness and ISA-indicators

Under scenario two (selective tree management), it is possible that species richness may accumulate, or ISA-indicators may be detected, as a consequence of historical continuity measured for an equivalent habitat-type. Many studies have demonstrated dispersal limitation for lichen epiphytes (Sillet & McCune, 1998; Hilmo & Såstad, 2001; Hilmo, 2002; Öckinger *et al*., 2005), and it is therefore possible that the longer the time over which suitable habitat persists within a woodland stand (increasing ecological continuity), the greater the likelihood of occurrence for a dispersal-limited species (Hanski, 1999). Additionally, once a dispersal-limited species occurs within a woodland stand, it may then persist within that stand so long as suitable habitat is consistently locally available: i.e. there is evidence for effective local (within-stand) dispersal, for species which are nevertheless dispersal-limited at larger (between-stand) scales (Hedenås *et al*., 2003; Hedenas & Ericson, 2008). The continuity of a given micro-habitat may therefore accumulate dispersal-limited species which contribute unique elements to the epiphyte flora.

Focussing on the oak tree as our target micro-habitat, this effect of dispersal-limitation on species richness and/or indicator species is not supported. Equivalent habitat (i.e. oak trees of a given size/age) within *Ancient* sites does not support more species than comparable habitat within *Recent* sites.

This negative evidence for differences in species richness and for the detection of ISA-indicators, may also run counter to scenario three (unaccounted for micro-habitat diversity). In scenario three, the added complexity of microhabitat heterogeneity in ‘old-growth’ woodlands may create opportunities for niche specialists (Lesica *et al.* 1991; Kuusinen & Siitonen 1998; Moning *et al*., 2009) – this may shift trends in species composition, increase species richness, and lead to the occurrence of ‘indicator species’ which are uniquely associated with ‘old-growth’ microhabitat. In scenario three we would not expect our sampling to provide an estimate of total species richness for a woodland site, but microhabitat heterogeneity at a stand-scale may nevertheless contribute increased species richness to locally co-occurring smaller-scale units, i.e. sampled oak trees.

We suggest that gradual accumulation of species richness through (i) the relaxation of dispersal-limitation by micro-habitat continuity (scenario two), and/or (ii) microhabitat heterogeneity (scenario three), may be off-set in oakwoods by successional processes associated with community saturation, which act to prevent a linear and indefinite accumulation of richness.

4.3 Tree-Scale Trends in Species Richness

We highlight previously important findings which would suggest species are able to accumulate indefinitely into unsaturated lichen communities: i.e. increasing species richness as trees age and grow larger, and with consequences at the site-scale. We then show that our results are counter to this evidence-base.

4.3.1 Species richness accumulates on older/larger trees

Much evidence at the scale of the individual tree has shown that the likelihood of occurrence and/or abundance of target epiphyte species increases with tree age (Uliczka & Angelstam, 1999; Johansson & Ehrlén 2003; Ranius *et al*., 2008; Belinchón *et al*., 2009; Johansson *et al*., 2010). This can be interpreted as a response to the time available for colonisation – species may accumulate on a tree as a function of their dispersal ability (Hedenås *et al*., 2003; Werth *et al*., 2006); or, given a relationship between tree age and tree size (dbh), species may accumulate as a consequence of increased habitat area for the capture of propagules (Lie *et al*., 2009).

At a community-scale, the richness of species has been observed to increase as a linear function of tree age/size (Holien 1997; Kantvilas & Jarman 2004; Lie *et al*., 2009; Möning *et al*. 2009).

4.3.2 Increasing tree-scale richness contributes to stand-scale richness

Beyond the tree-scale, species may accumulate into a woodland stand as a function of continuity. Thus, the longer a site is continuously wooded, then (i) the greater the number of increasingly old trees, with higher species richness values, including species which are specialists of old-tree microhabitats, and (ii) the greater the time available for dispersal onto trees within a stand. Therefore, older stands potentially accumulate greater species richness (Holien 1997; Kuusinen & Siitonen, 1998; Boudreault *et al*., 2000), including the greater representation of species that are dispersal-limited (Hedenås & Erikson, 2000).

4.3.3 Counter-evidence

In contrast to this linear increase in richness at the scale of the individual tree – and a subsequent increase in site-scale richness – we demonstrated for the sampled oaks a unimodal pattern in species richness, compared to tree age/size.

Where studies have attempted to independently assess the unique effects of size and age for entire epiphyte communities, results have been more complex and surprising than a simple linear increase. Nascimbene *et al*. (2009) demonstrated that species richness increased with tree age up to an asymptote at *c*. 250-300 yr, while it increased constantly with tree size (i.e. dbh and height). Johansson *et al*. (2007) suggested that the relative importance of age and size in controlling richness may be age dependent, with age the relatively more important variable on trees up to 65 yr, and with richness declining slightly on older trees. Similarly, we show that the lichen epiphyte richness on oak was positively related to tree size and age, but that an interaction was responsible for a decline in species richness beyond a size/age threshold of *c*. 100 yr. There is evidence from aspen in Scotland (*Populus tremula*) that species density on a trunk (the number of epiphyte species per unit area) may decline as a tree ages and grows (Ellis, unpublished data). It is possible therefore that up to a certain size, a tree's secondary growth (expanding dbh) may compensate for the local decline in species density through an increase in habitat area, but that for maturing trees the increase in surface area no longer compensates for a simultaneous decline in species density.

Ultimately, this decline in lichen epiphyte richness can be attributed to successional processes occurring on the tree. Tree age may control compositional variation through an effect on bark microhabitats (Kantvilas & Minchin 1989; Bates, 1992; Kuusinen, 1994; Ranius *et al*., 2008; Fritz *et al*., 2009; Jüriado *et al*., 2009; Johansson *et al*., 2010). We show that this age effect is part of a wider template of environmental trends, possibly including the effect of soil chemistry (pH and nitrogen content) on bark chemistry (Gauslaa 1985; 1995; Gustafsson & Eriksson 1995; Kermit & Gauslaa 2001), local trends in humidity, reflected by soil moisture (Kenkel & Bradfield 1986; Radies *et al*., 2009), and canopy closure and shading (Kuusinen, 1994; Gustaffson & Eriksson, 1995; Jüriado *et al*., 2009; Möning *et al*., 2009). Additionally, age effects include shifts in species trait-groups, with communities subject to autogenic succession that may also explain species richness trends (Stone 1989; Ellis & Coppins 2007b; Lewis & Ellis 2010): e.g. the out-competition of diverse sexually-reproducing crustose lichens by asexual crusts, foliose macrolichens and bryophytes, and, as a tree progressively becomes older, the dominance of bryophytes, associated with *Lepraria* spp.

4.4 Qualitative Indicator Species

In contrast to scenario one (see above), both scenarios two and three may explain the sampling pattern for WSIEC indicators. Thus, the occurrence of WSIEC indicators in *Ancient* sites may be explained by un-sampled microhabitat heterogeneity, and its continuity; facilitating the sporadic colonisation of these species into suitable microhabitat on oaks within the same site. Additionally, the local colonisation of WSIEC indicators from a source

(*Ancient*) to a sink (*Recent*) site is supported by the statistically greater abundance of these species in *Ancient* compared to adjacent *Recent* sites.

4.4.1 Increasing the ecological resolution of indicator species

Although not always clearly partitioned in the ecological literature, we believe the alternative scenarios required to explain our results help to highlight the critical separation of 'historical continuity' and 'old-growth structure' as ecological factors that are sometimes but not always correlated. In support of this argument, we found no convincing evidence for a meaningful difference in the demography (population age structure) of oaks in sites with assumed different levels of historical continuity, and – testing for paired sites – accounting for potential regional contrasts. Tree-ages at a given population interval, for any given *Recent* site, may tend to be older or younger than those in an *Ancient* site with equal likelihood. A key finding of this study is therefore that the tree population structure of our sampled *Ancient* sites – even assuming these sites have been wooded for many centuries and possibly millennia – may be fundamentally similar to that of recently regenerated woodland (*c*. < 150 yr old).

This highlights an opportunity for the refinement of 'qualitative indicator species'. For example, what are lichen indicator species telling the user, about the relative importance of the continuity of the woodland, with respect to dispersal-limitation and time, or the occurrence of old-growth microhabitats? These features – temporal continuity and old-growth structure – are two critically important, but potentially contrasting factors in assessing woodland management/conservation (see above), and they may be confounded in the non-critical interpretation of indicator species. For example:

- A site may have long historical continuity, but an apparent absence of old-growth structure (as might be assumed for our samples), and a community of lichens that is fundamentally similar to a recently regenerated site.

- Alternatively, over what time-frame might a site that is young, but managed to 'mimic' old-growth structure, develop a different and more diverse epiphyte community (including 'indicator' species)?

- Or, to what extent does the ecological continuity of specialist 'old-growth' microhabitats contribute to a community difference?

Epiphyte Indices are potentially useful tools in conservation, though should be improved by increased ecological scrutiny: e.g. providing a discriminatory score which quantifies the relative importance of, and interaction between, ecological continuity (pure time) and old-growth structure (microhabitat) in controlling the presence-absence of lichen epiphytes.

4.5 General Patterns of Species Composition

As with species richness and our ISA-indicators, we found no effect of stand continuity on general patterns of community composition. In contrast, numerous studies have observed the association of cyanolichens (including tripartite species) with stands comprising larger/older trees (Kuusinen, 1994; Kuusinen, 1996; Cleavitt *et al*., 2009), low management intensity (Aragón *et al*. 2010) and/or old forest stands (Lesica *et al*. 1991; McCune 1993; Kuusinen 1996; Campbell and Fredeen 2004; Berryman and McCune 2006). However, our *Recent* and *Ancient* sites are structurally similar, and neither may be expected to have a rich community of oceanic species, based on previous evidence. However, Ellis & Coppins (2007a, 2009) have suggested that cyanolichens, and associated oceanic species (e.g. within the '*Lobarion*'), become less restricted in their micro-habitat specificity towards an increasingly optimal climate. The evidence from this study also suggests that – so long as species occur locally within a 'source' site – a majority of characteristic oceanic epiphyte species are able to easily colonise between closely adjacent stands within Scotland's hyper-oceanic climate, and do not require extreme long-continuity in the ‘sink’ site, or complex old-growth structure.

Accordingly, our sampling captured representative examples of ‘oceanic’ epiphyte communities in *Recent* sites: e.g. species within the genera *Collema*, *Degelia*, *Hypotrachyna*, *Lobaria*, *Pannaria* etc. This underlies the mobility of these species within an optimum climate, contrasted with their application as old-growth indicators in more continental climatic settings. It suggests that, given the correct spatial setting at a local scale, globally-restricted oceanic epiphyte communities will develop at sites along Scotland’s west coast in regenerating forest – though spatial proximity to local propagule sources is a critical factor.

4.5.1 Spatial proximity

The identification of spatial proximity between source and sink sites, as a key factor affecting species composition, is strongly relevant to SNH’s national conservation strategy for Atlantic oakwoods. Thus, adjacent paired sites tended to be similar in terms of epiphyte composition, while there was no effect, or a weak effect, of spatial proximity at larger scales (i.e. among sets of paired sites). The absence of a larger-scale spatial trend is consistent with the similarities among sites in terms of their larger-scale environment: e.g. sites were purposefully located within the same Atlantic bioclimatic zone (cf. Fig. 1 and Fig. 4), and in a zone of low pollution (NEGTAP, 2001).

Comparability between paired sites points to local site factors structuring community composition. This includes the contrast between paired sites characterised by the ‘*Lobarion*’ community (STO-STB) and sites characterised by the ‘*Parmelion*’ (TIG-SOI), in woodlands that may be shaded and less acidic, and in well-lit, leached and more acidic sites, respectively (James *et al*., 1977). It also suggests that regenerating woodlands may ‘pick-up’ the flora of neighbouring extant woodlands. Paired sites may therefore have influenced each other through a localised ‘propagule rain’, i.e. source-sink, or mass effects related to propagule density (Hedenås & Erikson, 2008), while contrasting sets of paired sites may be positioned at a scale beyond local dispersal, being influenced by stochastic long-distance transport.

A strategy to maintain epiphyte diversity through forest regeneration might identify a suit of extant woodlands along a continuum in terms of their similarity/dissimilarity in epiphyte composition. Regenerated woodland may be positioned around these sites to buffer compositional differences, and intercalated between these woodlands, (increasing alpha-diversity): with the net effect of maximising and maintaining beta-diversity.

5 CONCLUSIONS

Our results lead to the following sequence of conclusions/recommendations:

1. For our twelve carefully selected sample sites – and which we believe to be representative of oakwoods more generally – the demography of oaks in *Ancient* sites is structurally similar to those of *Recent* sites: as a consequence, there is no evidence for an effect of historical continuity on epiphyte composition or richness. This structural similarity is attributed to a period of intensive management during late-18th and early-19th Century, possibly including clear-felling.

2. This finding helps to bring into focus a key difference between 'historical continuity', as recognised by the Ancient Woodland Inventory (i.e. the unbroken occurrence of trees on a site), and 'old-growth woodland', which is *Ancient* woodland that retains the structural properties of unmanaged or less intensively managed forest. Alternatively, 'old-growth' may include woodland of any age that has been artificially modified to emulate undisturbed forest.

3. Our finding of no difference in epiphyte communities – between *Ancient* and *Recent* sites – is specific to oak as the dominant tree species. It remains possible that sites with long historical continuity may retain other old-growth attributes, e.g. a greater diversity of companion tree species, a greater proportion of rare (and therefore unsampled) very old oak trees (> 200 yr), or greater volumes of deadwood etc. ***Patterns in these old-growth attributes, and their relationship with historical continuity and epiphyte richness need to be further investigated***.

4. This could be achieved by using the same and new sample sites, and including measures of woodland structural diversity, coupled with systematic epiphyte sampling from representative substrata**. *We suggest that this it would be useful to undertake such an investigation including the further quantification of indicator species sensitivity*.**

5. We demonstrated that species composition varies spatially – i.e. spatially-close, paired old-growth sites tended to be similar to each other in species composition. ***This suggests that existing epiphyte diversity would benefit from regeneration that is targeted to a spectrum of sites with contrasting lichen floras***. Regenerated sites may be expected to 'pick-up' the flora of closely associated *Ancient* sites – including the 'typical' elements of oceanic epiphyte communities – therefore increasing ecological resilience.

6. The study has also provided important new information of the pattern of tree-scale richness (on the lower trunk) during succession: i.e. a unimodal response to tree age and size, probably controlled by community successional processes. This suggests oceanic epiphyte communities become saturated, restricting the accumulation of species richness on older and larger trees.

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APPENDIX ONE – SPECIES LIST

Abrothallus bertianus
Abrothallus microspermus
Abrothallus parmeliarum
Anisomeridium biforme
Anisomeridium polypori
Anisomeridium ranunculosporum
Anisomeridium viridescens
Antennulariella lichenisata
Arthonia anombrophila
Arthonia cinnabarina
Arthonia didyma
Arthonia elegans
Arthonia mediella
Arthonia muscigena
Arthonia radiata
Arthonia spadicea
Arthonia vinosa
Arthopyrenia analepta
Arthopyrenia fraxini
Arthopyrenia salicis
Arthrorhaphis aeruginosa
Bacidia absistens
Bacidia caesiovirens
Bacidia squamellosa
Biatora britannica
Biatora vernalis
Biatoropsis usnearum
Buellia disciformis
Bunodophoron melanocarpum
Byssoloma marginatum
Calicium lenticulare
Caloplaca ferruginea s. str.
Candelariella reflexa
'Capronia aff. *epilobarina'*
Catinaria atropurpurea
Celothelium ischnobelum
Cetrelia cetrarioides
Cetrelia monachorum
Cetrelia olivetorum s. lat.
Chaenotheca brunneola
Chaenotheca trichialis
Chrysothrix candelaris
Chrysothrix flavovirens
Cladonia chlorophaea s. lat.
Cladonia coniocraea
Cladonia diversa
*Cladonia macilenta/polydactyla**
Cladonia pyxidata
Cladonia ramulosa
Cladonia squamosa var. squamosa
Cladonia squamosa var. subsquamosa
Cliostomum griffithii
Collema furfuraceum
Cystocoleus ebeneus
Dactylospora 'parasitaster'
Degelia atlantica
Degelia plumbea
Dimerella lutea
Dimerella pineti
Endococcus sp.
Eopyrenula grandicula
Evernia prunastri
Fellhanera duplex
Fellhaneropsis vezdae
Flavoparmelia caperata
Fuscopannaria sampaiana
Gomphillus calycioides
Graphina anguina
Graphis elegans
Graphis scripta
Gyalideopsis muscicola
Homostegia piggotii
Hypogymnia physodes
Hypotrachyna laevigata
Hypotrachyna taylorensis
Intralichen cf. christiansenii
Intralichen sp.*
Jamesiella anastomosans
Japewiella tavaresiana
Kalchbrenneriella cyanescens
Lecanactis abietina
Lecanora albellula agg.
Lecanora chlarotera
Lecanora confusa
Lecanora expallens
Lecanora jamesii
Lecanora symmicta
Lecidea doliiformis
Lecidea sanguineoatra
Lecidella elaeochroma f. *elaeochroma*
Lepraria caesioalba (cf.)
Lepraria incana s. str.
Lepraria jackii s. lat.
Lepraria lobificans
Lepraria rigidula
Leptogium brebissonii
Leptogium cyanescens
Leptogium teretiusculum
Lichenoconium erodens
Lichenodiplis lecanorae
Lichenomphalia cf. *umbellifera*
Lobaria amplissima
Lobaria pulmonaria
Lobaria scrobiculata

Lobaria virens
Lopadium disciforme
Loxospora elatina
Megalaria pulverea
Melanelia fuliginosa subsp. glabratula
Melaspilea ochrothalamia
Melaspilea sp. B
Menegazzia terebrata
Micarea adnata
Micarea alabastrites
Micarea byssacea
Micarea cf. *micrococca*
Micarea cinerea f. *cinerea*
Micarea coppinsii
Micarea peliocarpa
Micarea stipitata
Micarea synotheoides
Micarea viridileprosa
Micarea xanthonica
Mycoblastus caesius
Mycoblastus sanguinarius f. *sanguinarius*
Mycomicrothelia confusa
Mycoporum antecellens
Nephroma laevigatum
Nephroma parile
Nigromacula uniseptata
Normandina pulchella
Ochrolechia androgyna
Ochrolechia cf. *microstictoides*
Ochrolechia tartarea
Opegrapha atra
Opegrapha herbarum
Opegrapha multipuncta
Opegrapha niveoatra
Opegrapha sorediifera
Opegrapha varia
Opegrapha vulgata
'Ophiobolus pannariae'
Pachyphiale carneola
Pannaria conoplea
Pannaria rubiginosa
Paranectria sp. *('parvulae')*
Parmelia ernstiae
Parmelia saxatilis
Parmelia sulcata
Parmeliella parvula
Parmeliella triptophylla
Parmotrema crinitum
Parmotrema perlatum
Peltigera collina
Peltigera hymenina
Peltigera membranacea
Peltigera praetextata
Pertusaria albescens var. *albescens*
Pertusaria albescens var. *corallina*
Pertusaria amara f. *amara*
Pertusaria hemisphaerica
Pertusaria hymenea
Pertusaria leioplaca
Pertusaria multipuncta
Pertusaria pertusa
Phaeosporobolus usneae
Phlyctis argena
Phoma lobariae
Placynthiella icmalea
Platismatia glauca
Plectocarpon lichenum
Polychidium dendriscum
Porina coralloidea
Porina leptalea
Punctelia reddenda
Punctelia subrudecta s. str.
Pyrrhospora quernea
Ramalina farinacea
Rinodina efflorescens
Roselliniopsis tartaricola
Schismatomma quercicola
Sphaerophorus globosus
Sticta fuliginosa
Sticta limbata
Sticta sylvatica
Stigmidium arthoniae
Strangospora microhaema
Strigula thelopsidoides
Taeniolella sp.
Thelotrema lepadinum
Trapelia corticola
Trapeliopsis flexuosa
Trapeliopsis pseudogranulosa
Usnea cornuta
Usnea filipendula
Usnea flammea
Usnea fragilescens var. *fragilescens*
Usnea rubicunda
Vouauxiella lichenicola
Wentiomyces lichenicola subsp. *bouteillei*

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Scottish Natural Heritage
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