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Can epiphytic lichens of remnant Atlantic oakwood trees in a planted ancient woodland site survive early stages of woodland restoration?

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Abstract

Key message: Epiphytic lichens of remnant Atlantic oakwood trees, enclosed within a recently planted conifer matrix, show ability to survive early stages of woodland restoration (conifer removal).

Context: Atlantic oakwood, ancient semi-natural woodland (ASNW), supports important epiphytic lichens. Fragmented ASNW, historically in-filled with conifers, are now being restored to reflect ASNW tree and ground flora character. Concerns exist that sudden and total removal of the conifer matrix, will be detrimental to the epiphyte diversity of remnant trees retained within the former plantation.

Aims: Here, we ask whether an unintended consequence of habitat restoration is the loss of epiphyte populations on remnant trees.

Methods: Dynamics of ground flora development were studied at one 50 hectare site on the west coast of Scotland using indicator species occurrence and species traits. Change in cover of lichen species was determined and lichen vitality was assessed in two *Lobaria* species using chlorophyll fluorescence as a proxy. Assessments pre-, post- and nine years after conifer removal were made in plantation areas (containing remnant oak trees) and ASNW areas.

Results: Re-vegetation of the ground flora was predominantly by ASNW vegetation. Species richness and occurrence of native woodland indicator species increased and the community showed stronger competitor traits. Lichen vitality was initially reduced but recovered. Tests showed change in the abundance of key lichen species and lichen community diversity was non-significant despite the loss of four lichen species on remnant trees..

Conclusion: Ground flora dynamics indicate site recovery was underway within eight years of restoration activities and epiphytic lichens although variable in response were in this study largely unaffected, this restoration approach could be appropriate for other Atlantic oakwoods where lichen conservation is an objective.

Introduction

Forests have been modified by human activity, with plantations comprised of productive species replacing natural forests (FAO 2016). Natural and native forests are considered to have high conservation value when they have long temporal continuity (Nordén et al. 2014) and those whose continuous existence can be traced back to a threshold date (e.g. 1750 in Scotland) are termed ancient semi-natural woodlands (ASNW) (Forestry Commission, 2017). Human intervention is omnipresent in the histories of European forests (Bradshaw et al. 2015), resulting in forest fragmentation, stand structure and composition homogenization, as for example in the ASNW of *Quercus* and *Fagus* of western Europe, and un-fragmented ASNWs in Scotland have often been managed for centuries (Scottish Natural Heritage, 2011; Verheyen 1999; Rackham, 1989). More recently, in-fill planting (inter-planting with or without removal of remaining ASNW fragments/trees) with productive species, as dictated by forest policy of the mid-20th Century, has further modified fragmented ASNW (Pryor et al. 2002). The resulting woodlands are termed PAWS (plantations on ancient woodland sites). The planting of non-native conifers represents a sudden and substantial change to ASNWs (Thompson and Hope, 2005). Over time, detrimental impacts of such planting can result from over-shading of remnant woodland patches by mature conifers (Barbier et al. 2008) and changes such as increased soil acidity (Augusto et al. 2015) and lower water availability (Barbier et al. 2009), thus affecting understory development (Ferris et al. 2000; Bergès et al. 2017). The degradation of PAWS is considered so extreme as to make them unsuitable for forest specialist and ancient woodland indicator species for several centuries following restoration (Naaf and Kolk, 2015; Kolk and Naff, 2015).

Ecological restoration management aims to restore the community and the necessary ecosystem components (Young 2000). Targets for habitat restoration frequently include restoring a characteristic assemblage of the relevant species (e.g. indicator species of the target habitat) in addition to continued development of the habitat towards a restored state, and resilience to perturbation (SER 2004; Shackelford et al.

2013). Restoration success is frequently assessed using vascular plant species (e.g. woodland canopy species and ground flora) and diversity, and occasionally by use of growth form and growth traits to elucidate succession and community function (Grime 1977; Polley et al. 2005; Pfestorf et al. 2013; Kirby et al. 2017).

Restoration of Atlantic ASNW oakwood is a priority conservation action as the habitat is a European Union Habitats Directive habitat (Annex I habitat: 91A0 "*Old sessile oak with Ilex and Blechnum in British Isles"*), and its conservation status currently ranges from 'unfavourable' to 'bad'(ec.europa.eu consulted June 2017; JNCC.defra.co.uk consulted July 2017). "Favourable condition" for priority woodland habitats in the UK is achieved when the canopy comprises 95% site native species (Brown et al. 2015). Therefore, in response to the maturation of many of the non-native conifer crops planted on PAWS, recent forest policy has been to initiate a return to site native species canopy dominance by removing these conifers (Brown et al. 2015).

Within PAWS, the ground flora of ASNW Atlantic oakwood areas and remnants provide the indicator species, measures of richness and profiles of traits against which progress of PAWS restoration towards Annex 1 Habitat 91A0 can be assessed (Kirby et al. 2017; Shackelford et al. 2013). However, the actions undertaken in restoration may be detrimental to alternative guilds occupying the oakwood remnants which could be considered a conservation priority. Internationally important lichen assemblages develop in 91A0 habitat (James et al. 1977), the richest being in the Scottish Highlands as indicated by diverse *Lobarion* communities. Of the 706 woodland lichen species present in the UK, 517 are reported only in Atlantic woodlands. Nineteen of the total 706 species are reported as being of UK international responsibility, often found upon remnant trees of Atlantic oakwoods (Coppins and Coppins 2005). Of the lichen species used to grade the 'ancient woodland' characteristics of deciduous woodlands in the British Isles (providing an *Index of Ecological Continuity*), a subset of 50 species form the *Western Scotland* community, particular to the mild, wet, Atlantic climate experienced along much of lowland and coastal western Scotland (Coppins and Coppins 2002). In a woodland ecosystem, removal of plantation trees (felling) can lead to sudden alterations in the water table, light availability and climatic exposure (e.g. wind, frost), and therefore be detrimental to woodland ecosystems by changing both abiotic conditions (e.g. temperature, humidity) and resource availability (e.g. light) (Knapp et al. 2014). Removal of the plantation trees represents a second period of perturbation for a PAWS (Thompson and Hope, 2005). Whilst gradual removal of plantation trees is anticipated to be less perturbing to the woodland ecosystem, operational and economic constraints of managing western fringe woodlands in Britain generally means that conifer removal has to be undertaken in a single operation (Brown et al 2015; Thompson and Hope, 2005). Thus unintentionally, lichens on the trees that are retained may be detrimentally affected by restoration action. Lichens can only photosynthesise when they are wet but are generally able to resist damage from high light levels and temperatures when in a desiccated state (Green and Lange 1995). However, for epiphytic woodland lichens, damage can occur even when the thalli are dry (Gauslaa and Solhaug 1999). For these lichens e.g. in the genera *Lobaria, Pseudocyphellaria* and *Sticta*, reduced vitality would therefore be expected to occur with changes in microclimate at forest edges. *Lobaria* species in particular have been used as the focal species in studies of lichen sensitivity to forest management changes, exhibiting physiological responses more rapidly than changes in lichen cover or presence (Renhorn et al. 1996; Palmqvist and Sundberg 2000).

In this study conifers were removed from an Atlantic oakwood PAWS in an attempt to restore the dominance of native species in the canopy and the ancient woodland ground flora communities. We anticipate that an unintended consequence of restoration management within the PAWS will be initial physiological stress to epiphytic lichens on the retained trees immediately following conifer removal, and eventual loss of the sensitive species (e.g. *Lobaria* species) in years subsequent to the restoration actions. Specifically, our objectives were to quantify the effects of conifer removal on: (1) ground flora composition and community traits as a means of assessing restoration progress and (2) epiphytic lichen vitality, cover and community diversity.

b. Materials and methods

Study site and Experimental Design

The study site is a Planted Ancient Woodland Site (PAWS) in Glencripesdale National Nature Reserve on the shores of Loch Sunart, North-West Scotland (56°40'N, 5°49'W)(Fig. 1a). It covers approximately 50 hectares at elevations of less than 60m above sea level. The PAWS consists of two types of woodland; firstly, fragments (>2ha in size) of ancient semi-natural woodland (hereafter referred to as *ASNW*) and secondly, areas of conifer plantation comprised of Sitka spruce *Picea sitchensis* (Bong.) Carrière*,* dating from a 1971-1977 Forestry Commission plantation scheme (Fig. 1b), which we term *plantation*. Embedded within the *plantation* are additional small patches of ancient semi-natural woodland, which were kept when the plantations were established (hereafter refereed to as *remnants*) (size range 0.01-0.03 ha) (Fig. 1b). The *ASNW* (and *remnants*) is mainly comprised of sessile oak woodland (habitat 91A0) that typically occurs on impoverished acidic soils with an overstorey of *Quercus petraea*, *Q. robur*, *Betula pendula* and *B. pubescens* and an understorey containing *Ilex aquifolium* and *Corylus avellana.* The ground flora of these woodlands is strongly influenced by the oceanic climate of the site (Fig. 1, Appendix A in supplementary material) leading to dominance by ferns, mosses, lichens and acidophilous grasses (Rodwell 2005). Climatically, Glencripesdale may be representative of many oak woodlands in Scotland, as climatic indices for other oak woodland sites (Fig. 1a) show a small range in values and from which the values for Glencripesdale rarely differ (see Table 1, Appendix A in supplementary material for details).

Fig. 1 is located here

The objectives of the restoration treatments was to return the site to one primarily occupied by site native tree species by retaining native trees and creating gaps of sufficient size for natural regeneration (Thompson and Hope, 2005). The cost of the intervention was required to be largely offset by timber sales so as much timber as possible had to be removed from the site. All of the conifer trees had to be felled in one intervention due to the anticipated instability of the crop. Experience of management of plantations on similarly exposed sites showed that thinning operations would very likely lead to wind damage and uprooting of the remaining conifer trees (Gardiner and Quine, 2000). Further, the site terrain afforded insufficient access for repeat interventions thereby precluding gradual thinning of the crop (Thompson and Hope, 2005). Restoration treatment was carried out in the *plantation* areas by felling all the conifer trees. We refer to the felled areas as *former plantation*. Care was taken during felling operations to avoid damaging the *remnants* and these were retained within the *former plantation*. Felling took place during the autumn of 2007 at which time the conifer crop had achieved an average basal area of 62 m^2/ha. Felling was carried out mechanically by a wheeled harvesting machine, access routes or racks were cut in the *plantation* and conifer trees were removed by the harvester stationed where possible on the racks. The timber was removed from the site but thinning residues (branches and foliage from the felled trees) were left on site and some were used in the construction of brash mats in the racks for the harvester to move over, thereby protecting the soil from erosion. No interventions were applied to the *ASNW* or the *remnants* during the study.

To assess restoration success, ground flora assessments were carried out to compare the change over time of communities in the *former plantation* and communities within the *remnants*. Ground flora assessments were made in 72 permanent quadrats, 18 in the *remnants*, 54 in the *former plantation*. To understand if there were unintended consequences of restoration management on conservation priority species, the impact of conifer removal on epiphytic lichen communities was assessed from measurements taken of lichens on trees within the *remnants* within the *former plantation*, as compared to in the *ASNW* (Fig. 1b). Physiological measurements were taken on 52 *Lobaria spp.* thalli (32 in *remnants* and 20 in *ASNW*) and species composition and species cover was assessed from 22 precisely relocated patches of long continuity woodland lichen communities (Thompson and Hope, 2005) on different tree stems (14 in *remnants*, 8 in *ASNW*). Based on assessment of lichens on trees which remained throughout the restoration, we will consider failure to survive PAWS restoration as both a reduction in lichen cover on the overall sample of *remnant* trees compared to *ASNW* trees, and a permanently compromised physiological function of the focal lichen species supported by the trees. A reduction in lichen community diversity on the overall sample of *remnant* trees compared to *ASNW* trees will further indicate that the lichens are failing to survive.

Ground Flora assessment

The ground flora was assessed by estimating total percentage cover of all species of vascular plants, mosses and liverworts, in the *former plantation* and *remnants* at 6 plots located across the site. Each plot consisted of three, parallel transects (3m apart, 15m long) running from the *remnant* into the *former plantation*, with four quadrats (0.5m x 0.5m) positioned along each. The first quadrat (Q0) was positioned inside the *remnant* at 6m from the *former plantation* boundary (ecotone), and the remaining 3 quadrats inside the *former plantation* at 3m (Q9), 6m (Q12) and 9m (Q15) from the boundary (Fig. 1b). Assessments were made immediately after conifer removal (2008) and again in 2016. The locations of the transects were recorded *via* GPS and the start of each transect within the *remnant* delimited with marker pegs.

Lichen assessment

Chlorophyll fluorescence (CF) yield to assess lichen physiology was measured for *Lobaria pulmonaria* and *L. virens*, each on 2 thalli located on the low stems or branches of 10 trees in the *remnants* (9 of which supported *L. virens* and seven supported *L. pulmonaria*) and five *ASNW* trees (all five trees supported both lichen species). Three readings were taken on each thalli at each sample time. Individual thalli were identified using plastic pegs and were revisited on each occasion. The mean diameter of trees at breast height was 29.9 cm (± 14.32 SD). Chlorophyll fluorescence is a rapid, non-destructive ecophysiological tool that allows measurements of photosynthetic capacity and light utilisation to be made *in situ* which can detect reductions in plant vitality before any visible signs are evident (van Kooten and Snel 1990) and is commonly used as a proxy measure of lichen vitality (MacKenzie et al. 2001). Measurements were taken at three time-points: in the autumn in the year prior to, and autumn following, conifer removal (2007 and 2008, respectively). This allowed us to assess short-term changes, and in the autumn nine years after conifer removal (2016) to assess mid-term changes. CF measurements were taken at ambient temperatures using a pulse amplitude moderated (PAM) chlorophyll fluorimeter (Walz MiniPAM, Wlaz GmBH, Effeltrich, Germany). Autumn sampling ensured that the opportunity for thalli hydration was enhanced by time of year. Details on chlorophyll fluorescence measurements and calculation are included in the supplementary material (Appendix A).

Changes in lichen community diversity and cover in remnants and ASNW between 2007 (pre-conifer removal) and 2016 (9 years after conifer removal) were assessed using fixed-point photographs of patches (22) of long continuity woodland lichen communities on different tree stems (14 in *remnants*, 8 in *ASNW*) which remained throughout the restoration. The sample patches did not contain the thalli tested for chlorophyll fluorescence but sample patches and sample thalli were usually on the same stem.

The lichen communities were determined by Thompson and Hope (2005) by means of comparing a species inventory with species listed in the West of Scotland Index of Ecological Continuity and the New Index of Ecological Continuity (Coppins & Coppins, 2002) (Table 2, Appendix A in supplementary material). In 2007, a sample of 39 lichen community patches (24 in *remnants*, 15 in *ASNW*) were marked and assessed. Selection aimed to achieve a sample of tree stems from across the site also with accessible *Lobaria pulmonaria* and *L. virens* thalli providing an equal sample of theses species within the *remnants* and *ASNW*. Around half (58% in *remnants*, 53% in *ASNW*) of the community patches were relocated in 2016 and rediscovery rates of *L. pulmonaria* and *L. virens* dominated patches were similar in the *remnants* and *ASNW*. From the field notes and site photographs we determine that the wood supporting four patches in the *remnants* and four in the ASNW was lost through branches or small stems snapping and subsequently being removed (decaying); loss or obscurity of patch markers (plastic nails) on the stems accounting for the remainder of 'missing' patches.

A PVC 0.04m^2 frame was fixed around each patch with three plastic nails set into the bark; for smaller lichen patches a half-frame measuring 0.02m^2 was used. The sample patches were located at surveyor height (between 52 cm and 273 cm from base of tree) and photographed with a 10 megapixel digital field camera. The frame was removed to be used on another tree, but the nails were left *in situ* for precisely locating samples in the next survey. The photographs were corrected for parallax with the Windows utility Perspective Image Correction and processed with Trimble's ©E-cognition in order to extract the surface areas of the different lichen species; details are presented in Appendix A, supplementary material.

Data analysis

Evaluating restoration success through ground flora species colonisation and trait composition

Evaluating change in ground flora community

We determined occurrences of all species present in the *former plantation* and *remnants* quadrats in the spring immediately after felling (2008) and 9 years after felling (2016). We counted the frequency of quadrats containing tree seedlings and saplings and of species indicative of site potential for native woodland establishment and development. The latter correspond to *precursor vegetation* and *desired invaders* as defined by Rodwell and Patterson (1994) in the National Vegetation Classification

(NVC) woodland types (W7, W9, W11 and W17) that constitute the ASNW at the study site. *Precursor species* represent open land vegetation able to become components of corresponding woodland, and the *desired invaders* are woodland specialists that arrive once the canopy is established (Rodwell and Patterson 1994). These were combined and referred to hereafter as *indicators.* Firstly, using data for all species, the number of different species present and the mean and standard deviation for each quadrant was calculated for 2008 and 2016. A paired t-test was used to compare means at each time-point with Shapiro-Wilk normality tests performed to check for normal distributions of data (all tests < 0.05). Secondly, using data for indicator species only and separated in into *remnant* and *former plantation* quadrants, the number of species observed in each transect and plot was summed and analysed as count data using Poisson regression. For *remnants*, general linear models were fitted with time as a fixed factor to test whether the number of species observed had increased from 2008 to 2016. For the *former plantation* analyses, as three different quadrats were sampled, quadrat was fitted as a random effect in a mixed effects general linear model using the 'lme4' package in R (Bates, 2015). Tests for overdispersion were carried out by using a chi-square test on the ratio of the Pearson's residuals squared to the residual degrees of freedom. No overdispersion was detected.

Evaluating change in traits

In our study, we anticipate that resources for vascular plant growth will change in response to removal of conifers in the *former plantation* but not for those in the *remnants,* with species requiring/utilizing higher levels of light (as canopy removed) and nitrogen (from felling residues) becoming more abundant in the *former plantation*. Accordingly, we anticipate that the plant community composition will change to include species with certain characteristics. Specifically, change is likely to be from a community able to tolerate the stress of low resource availability to one with traits for competitive growth or faster resource use ability (such as shown by competitive species) in the *former plantation*, whilst the pre-existing mixture of strategies may be maintained in the *remnants* where there is less change in resources. We used systems established in the literature as being of relevance to restoration (e.g. Curt et al. 2003; Fukami et al. 2005; Douda et al 2017), to describe the traits of each species occurring in the study site (Grime 1977; Ellenberg et al. 1992). Ellenberg's indicator values are ecological traits describing plant requirements and can be used to characterize variations in plant species habitat niches. Grime strategies are species groups based on shared traits, which can be used to characterize variations in ecological trajectories of plant communities. Vascular plants were attributed revised Ellenberg values for British plants (Hill 1999) for light, moisture and nitrogen. Grime strategies (Grime 2007) are only available for vascular plants, which were classified as competitive (C), stress-tolerant (S) or ruderal (R) or a mix of two (CS, CR, SR) or three strategies (CSR).

In order to test whether species trait or composition differed between *former plantation* and *remnant* from 2008 to 2016 a fourth corner and RLQ analysis was performed using the 'ade4' package in R (Dray et al, 2007). An R matrix was constructed by assigning *former plantation* or *remnant* for 2008/2016 to each of the 144 transects. The Q matrix contained Ellenberg values and Grime strategy C-S-R values for the 53 species which had both of these variables available (Table 3, Appendix A in supplementary material). C-S-R values were calculated for each species as described in Hunt et al. (2004). A single C, S and R value was assigned which summed to 1, e.g., a C species would have 1,0,0 values respectively, whereas a CR plant would be assigned values of 0.5,0,0.5. An L matrix was created containing species abundance for each of the 53 species in each transect.

A correspondence analysis was performed on the L matrix and a principal components analysis on the Q matrix. A multiple correspondence analysis was applied to the R matrix. A fourth corner analysis (Legendre et al, 1997) was then applied to test whether there were associations between species traits and environmental variables (*remnant* vs *former plantation*). The association between each species trait and each environmental variable were calculated and p-values corrected using the false discovery rate (FDR) procedure.

Evaluating the impact of clear-felling on lichen vitality, cover and diversity

Assessment of lichen vitality

Chlorophyll fluorescence (CF) yield in lichens is sensitive to temperature (Palmqvist and Sundberg 2000) so only pairwise comparisons of yield should be made at each assessment time and not between different assessment times. Accordingly, independent t-tests were performed to compare the mean yield between *L. pulmonaria* on trees in *remnants* versus *L. pulmonaria* on trees in *ASNW* and *L. virens remnants* versus *ASNW*. T-tests were carried out for each time-point separately. Levene's tests were carried out to check for homogeneity of variance and where these tests were statistically significant, Welch's t-tests for samples with unequal variance were performed. Analysis was conducted in R (version 3.5.2, R Core Team 2018), with graphics produced using ggplot2 in R (Wickham, 2016).

Assessment of changes in lichen cover and community diversity

Difference in cover (in cm^2) between 2007 and 2016 was calculated for each lichen in each sampled patch. For frequently occurring lichens (in 5 or more sample patches in 2007 or 2016) and for all lichens as a group, a 95% confidence interval for mean difference of cover was estimated, with a value of zero being assigned where a species was absent in 2007 and 2016. The 'boot' package in R was used to perform boostrapping, with over 5000 replicates and with confidence intervals calculated using the adjusted bootstrap percentile (BCa) method (Cantly and Ripley, 2017; Davison and Hinkley, 1997). Bootstrapped means and confidence intervals are shown for *ASNW* and *remnants* for each lichen species and the lichen group.

Following the recommendations of Reemts and Eidson (2019) we used the diversity metrics of species richness and average conservatism, to assess change over time and difference between *ASNW* and *remnants*, respectively. Average conservatism reflects the contribution made to the community sampled by species considered as being specialists for the habitat under study. To calculate average conservatism we assigned coefficients of conservatism to each species encountered in our sampling based on their fidelity to Glencripesdale oak woodland. This was judged from their membership of the Glencripesdale lichen community described by Thompson and Hope (2005), and their role as ecological continuity indicators of oceanic oak woodlands, other Scottish oceanic woodlands and woodlands of long ecological continuity (Coppins and Coppins, 2002) (Supplemental Material, Table 2, Appendix A). Tests for differences between treatments and years in species richness and community average conservatism were performed using Mann-Whitney tests conducted in R (version 3.5.2, R Core Team 2018).

c. Results

Evaluation of change in ground vegetation and trait composition

Ground flora species richness

There was a significant increase in species richness of the ground flora between 2008 and 2016 in *former plantation* but not in the *remnants* (Table 1). The number of species doubled in the *former plantation* from an average of three to six species per quadrat and increased by 27% in the *remnants*.

Table 1 located here

Natural regeneration

One growing season following conifer removal, tree seedlings and saplings were found in 17% of quadrats in both *former plantation* and *remnants*, with native species being present in 60% of the occupied quadrats in the *former plantation* and all of the occupied quadrats in the *remnants*. In 2016, tree seedlings and saplings were recorded in 60% of the quadrats in the *former plantation* (89% of occupied quadrats containing native species) and 30% of the quadrats in the *remnants* (66% containing native species). Regenerating native species included (in descending order of frequency) *Betula pubesences/ B. pendula, Alnus glutinosa, Quercus petraea, Ilex aquifolium and Corylus avellana.* Sitka spruce was the only regenerating non-native species.

Ground flora indicator species

Overall, 26 ground flora species listed as *indicators* of site potential for native woodland establishment and development at the study site were recorded (Table 4 Supplemental Material, Appendix B). Twenty-one of these were present immediately after felling: 11 species in the *remnants*, 1 species in the *former plantation* and 9 species in both sample areas. By 2016, a further 5 *indicator* species were recorded at the site and a total of 11 *indicator* species appeared to have colonised a different sample area e.g. from *remnants* to *former plantation*. *Indicator* species count increased significantly from 2008 to 2016 in the *former plantation* (β =1.375, Std. Error = 0.169, p = < 0.0001) but not in the *remnants* (β =0.147, Std. Error = 0.181, p=0.42).

Interpretation of ground flora community composition using species traits

The three-table ordinations were applied on the ground flora dataset. The goodness of fit was determined by the correlation of RLQ axis with initial site-species table (L). A good correlation was observed between the first axis (0.53) and for the second axis 0.22 (Table 5 Supplemental Material, Appendix B). The stability of the link between the trait and environment association was analysed using a Monte-Carlo permutation test (20,000 permutations) (p < 0.03). The results of RLQ analysis validly represented the relationship between environment (location x year combinations) and plant traits. From the visual inspection of Fig.2, trait characteristics of the ground flora within the *remnants* are similar in both years but change in the *former plantation* between 2008 and 2016. In the *former plantation* in 2016 there is a positive association between species showing competitive traits and a negative association with species showing ruderal traits; in 2008 a positive association with species showing stress tolerance traits and low light requirements is indicated (Fig. 2 and Table 6, Supplemental Material, Appendix B).

Fig. 2 located here

Impact of clearfelling on epiphytic lichens

Short and mid-term effects on lichen vitality measured by chlorophyll fluorescence (CF) yield

In the autumn following conifer removal, significantly lower (by c.40%) CF yield was observed for both *L pulmonaria* in the *remnants* compared to the *ASNW* (Fig. 3, time-point 2). Although the difference in CF yield means is less pronounced prior to conifer removal, significant differences in CF yield were observed for *L. pulmonaria* (Fig. 3, time-point 1) on the *remnants* trees compared to those on *ASNW* trees; these effects were not seen for *L. virens*. Nine years following felling, CF yield was similar between the lichens on *remnants* and *ASNW* trees but *L. virens* generally showed a greater variability on CF yield than *L. pulmonaria* (Fig. 3, time-point 3).

Fig. 3 located here

Mid-term effects on lichen cover and community diversity

Overall, ten lichen species were recorded from the 22 sample patches (Table 2). In the *ASNW* the same seven species were recorded in 2007 and again in 2016 whereas in the *remnants*, 4 of the 9 species (*Ochrolechia androgyna, Platismatia glauca, Lichenoconium usneae and Stricta limbata*) disappeared. Of these, *Stricta limbata* had only been recorded on *remnant* trees. None of the lichen species disappeared from the *ASNW* trees (Table 2). Species persistence in the ASNW sometimes comprised the disappearance of a lichen from one patch and appearance in another (e.g. *Ochrolechia androgyna* and *Platismatia glauca*).

Lichen community average conservatism diversity was higher for the *remnants* compared to the *ASNW* in both 2007 (Mann-Whitney Test; U-statistic =27.0, $p < 0.05$) and 2016 (Mann-Whitney Test; U-statistic =30.0, $p < 0.05$). There was no change in species richness in either the *remnants* or the *ASNW* between 2007 and 2016 (Supplemental Material, Table 6, Appendix B).

Table 2 located here

Boot strapping of change in cover was conducted for lichen as a group and then specifically for *L. pulmonaria, L. virens*, squamules of unidentified species of *Cladonia* (Fig. 4).

All bootstrapped confidence intervals for *ASNW* and *remnant* sample patches overlap suggesting that changes in lichen cover are not attributable to the removal of conifer surrounding the *remnants*; however due to the low number of replicates it is difficult to draw firm conclusions from these data. Confidence intervals are large for the single species tested indicating a strong disparity in change between samples. Increases and decreases in lichen cover occurred in both the *ASNW* and *remnant* sample, however the trend of change in cover caused by the conifer removal for *L. pulmonaria* and all lichens as a group appears negative (reflecting decreases of 100 cm^2 or more in some patches), and for the lichens identified as *Cladonia* spp. as a positive change (Fig. 4).

Fig. 4 located here

d. Discussion

Overview

In the nine years following restoration management, re-vegetation of the *former plantation* occurred. Natural regeneration by primarily native species was recorded, and ground flora species richness and count of native woodland indicator species increased in the former plantation compared to the *remnants*. The plant trait analysis indicated communities in the *former plantation* had changed overtime whereas those in the *remnants* had not. Lichen vitality in the *remnants* was reduced following conifer removal relative to the *ASNW* but recovered within nine years. No mid-term change in lichen community diversity or lichen cover was clearly attributable to PAWS restoration.

Ground vegetation response measures of restoration success and timeframe of restoration

Restoring the characteristic assemblage of species of the reference ecosystem

Species-based assemblages are often evaluated by the study of vegetation because of its important trophic and biomass contribution, with composition being compared between restored and reference sites (Young 2000). Despite the short duration of our study relative to the timescales of woodland establishment, vegetation in the *former plantation* showed development towards a species assemblage characteristic of the *remnants*. Such an outcome has been shown to take place over periods of a century or more (Kolk and Naff, 2015; Naff and Kolk, 2015) but as Kirby et al. (2017) reported, ground flora resembling that of an oak woodland developed over a period of c.30 years close to rows of oaks, following restoration of mixed, Norway spruce-oak woodland. From this we conclude the proximity of remnants to former plantation at our study site is enhancing the rate of indicator plant colonization.

Continued development of the ecosystem

Consistent with the measures of restoration success (SER 2004; Shackelford et al. 2013), continued community development (e.g., changes in species and community traits) are seen at our study site following restoration management. Species richness increased in the *former plantation* and ecological traits changes indicated a response of the community to change in resource levels (e.g., light) and consequent community development reflected in plant strategies (Grime, 2007). Kirby (1988), observed three phases during restoration of ASNW: an initial increase of richness of ground flora, a decrease during the dense thicket stage and a further increase in the longer-term. We suspect that the *former plantation*, having shown a doubling in species richness following the conifer removal, was still in the first stage of restoration.

Differences in dominant strategies of plant communities at different successional stages would be expected following disturbance and recovery (Curt et al, 2003; Fukami, 2005). The clear-felling event changed the resource availability particularly in the *former plantation*.at the site (increased light) The ecological traits of the plant community reflect this and as we anticipated, competitive strategies appear to be expressed more strongly in the *former plantation* community in 2016 compared to the *remnants.* This response is consistent with previous studies which show that clear-felling initially stimulates vigorous plant growth, with an abundance of grasses on abandoned grassland invaded by conifers (Paul and Ledgard 2009), or bracken and bramble in lowland oak woodlands (Harmer et al. 2005). However, unlike these studies, we did not observe a reduction in plant diversity or woodland ground flora specialists (*indicators)* (Brown et al. 2015). In the years following this study, we would anticipate that the development of an overstorey at the study site would start to drive the community towards one expressing stress-tolerant and ruderal traits as these traits were expressed more strongly in the ground flora of closed canopy conditions in the *former plantation* (2008) and the *remnants* (Grime 1977). However, there are concerns that an abundance of competitive species may limit resource partitioning which could ultimately diminish final species diversity and limit resemblance of the *former plantation* to the target ASNW (Polley et al. (2005). Extrapolating the detail of these findings to other Atlantic oak woodland may be difficult as the response of ground vegetation to clear-felling is likely to vary according to initial composition and local-site factors (Knapp et al. 2014).

Resilience of restored ecosystem

Results from this study show that regeneration of former native woodland flora was occurring, indicating the resilience of the ecosystem. The rate of natural regeneration of trees was constant in the *remnants* and increasing in the *former plantation*. Recovery of woodlands is sensitive to the way in which harvesting is performed. Paul and Ledgard (2009) showed that increases in herbaceous vegetation were proportional to thinning, and the intensity of thinning rates affected the response in functional groups in longer-term assessments. Restoration by clear felling in one operation, as dictated by the site condition in our study, is a major perturbation but could be considered as a smaller disturbance compared to the inter-planting with conifers which occurred 40 years previously (Thompson and Hope, 2005). Like Kolk et al. (2017), we observe recovery of ground flora following this change in habitat type (albeit the transition between different habitat types was a of shorter duration in our study), indicating the resilience of the native woodland ecosystems to interventions and perturbations.

Overall, response of the vegetation at our study site following restoration appears to be consistent with the several indicators of restoration success. Signals of restoration success are clear from the colonization by specialist species (indicators),increased species richness and changes in the traits expressed, as they occur in the *former plantation* and not in the *remnants.* These findings suggest early stages of restoration have been achieved.

Lichen response

Chlorophyll fluorescence

Immediate changes in microclimate following conifer removal were sufficient to affect the vitality of the epiphytic lichens on the remnant native broadleaves and this concurred with findings of previous studies (Gauslaa and Solhaug 1996; Gaio-Oliveira et al. 2004). However, it appeared that the *Lobaria* species at our study site did not show permanently compromised physiological function, as suppressed lichen vitality was no longer evident after nine years. Like those adapted to deciduous woodlands elsewhere, lichens at our study site appeared to tolerate increased exposure to light resulting from the restoration treatments (MacKenzie et al. 2001; Gaio-Oliveira et al. 2004). Such physiological changes have been recorded as happening within as little as 13 months after the conifer removal (Gauslaa and Solhaug 1999).

Lichen cover and community diversity

Change in lichen cover overall on *remnant* trees retained after PAWS restoration was not clearly attributable to the removal of conifer trees, although trends in change of cover were recorded. The lichen community diversity remained higher in the *remnants* compared to the *ASNW* and showed no significant change in species richness at this mid-term assessment. This was despite the disappearance of four lichen species from the *remnants*. This would suggest that these species were affected by restoration treatment. However, losses and colonization occurred for the same species on ASNW trees, indicating the dynamic nature of populations. Taking into account the recovery of lichen vitality and the extent of change in lichen cover and diversity, survival of lichens to restoration treatment within *remnants* is indicated but not clear-cut. Resilience to such changes however has not been seen in other studies, with epiphytic old growth forest lichens affected by positioning *i.e.* forest edge compared to forest center and the negative effects of altered microclimate and mechanical damage (Gauslaa *et al.* 2019). Considering the impacts of PAWS restoration, our study showed that together, *ASNW* and *remnants* continued to provide suitable host tree species for many of the lichen species. This is despite the changes in environmental conditions brought about by restoration management, both of which may vary. Jüriado *et al.* (2008) showed that substrate type and tree species have a crucial effect on lichen diversity which outweighs the effect of environmental conditions in unperturbed sites. This is important as it is the native broadleaved trees and not the non-native conifers which need to be present if 'favourable' condition (canopy comprising 95% site native species) is to be achieved for this priority woodland type (Brown et al. 2015). Furthermore, the prospect for restoration and continuity of epiphyte assemblages at the site level appears good, as regeneration within the clearfelled areas is predominantly of site-native broadleaves and is close to *ASNW/remnants*. Our results highlight the importance of *ASNW* areas in lichen maintenance at this PAWS site following restoration as, with one exception, the ASNW lichen sample patches supported all of the lichens also found on the *remnants*. The unrepresented species was however recorded from *ASNW* from a wider site inventory (Thompson and Hope, 2005). Such proximity between potential/future host trees has shown to increase lichen diversity and abundance when comparing semi-natural pine and oak woodlands with adjacent planted stands (Humphrey et al. 2002) as it favours propagule dispersal, essential for maintaining lichen diversity (Ellis 2012). The mid-term survey indicated that lichen communities are dynamic within the entire PAWS restoration site. Different species have been shown to differ in recolonistation timescales, influenced by their habitat sensitivity (generalist or specialist), fecundity and longevity (Watts et al, 2020). It may take decades for the specialist elements of a woodland community to reach a dynamic equilibrium when little remains of the original woodland. This is not the case at our study site and any unintended consequences of restoration may be relatively short-lived. Continued monitoring of the site to provide further evidence is recommended.

e. Conclusion

Whilst this restoration assessment covered a relatively short timescale when compared to the natural regeneration cycle of an oak forest, our results are encouraging for restoration by removal of planted non-native conifers from mixed native woodland. Early stages of restoration have been achieved as evidenced by tree regeneration, and responses of the ground flora (species richness, indicator species and community traits). Our study has shown that epiphytic lichen communities can to some extent withstand environmental changes caused by PAWS restoration in the first nine years following intervention. However, changes created by restoration treatments are not inconsequential. Whilst all but one of the lichen species survived within the monitored site as a whole, four species were lost from the remnants. With continued woodland restoration, conditions for epiphyte lichen survival should not become less favourable (e.g. Palmer et al. 2005) provided a balance is struck between sufficient regeneration to create woodland conditions and high densities of saplings, threatening epiphytes by over shading (Leppik et al. 2011). Densities of sheep and red deer (which are ubiquitous throughout these habitats) will need to be carefully managed to allow continued regeneration, perhaps balanced with some judicious thinning to prevent overstocking of the woodland (Harmer et al. 2010). This study was conducted at a single site which limits generalization of the results. The study site is a coastal forest, which implies that it could be less sensitive to desiccation than other sites of the same woodland type located further away from the coast. Oceanicity is a defining feature of the European Atlantic Region as a whole and one which shapes lichen assemblage composition (Coppins and Coppins, 2002). There is estimated to be 59,000ha of PAWS in Scotland (Forestry Commission, 2013), 32,000 ha of which was surveyed as part of the native woodland resource, and of this a large proportion falls within the European Atlantic Region in the West Highlands (Patterson et al, 2014). Securing ancient woodland remnants and restoration of the matrix to native woodland will reap benefits to biodiversity in the long-term and help achieve goals set for habitat restoration in the Convention on Biological Diversity (Convention on Biological Diversity 2001; Benis et al. 2014).

f. References

Augusto L, De Schrijver A, Vesterdal L, Smolander A, Prescott C, Ranger J (2015) Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. Biol Rev 90:444–466. doi: 10.1111/brv.12119

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. For Ecol Manag 254:1–15. doi: 10.1016/j.foreco.2007.09.038

Barbier S, Balandier P, Gosselin F (2009) Influence of several tree traits on rainfall partitioning in temperate and boreal forests: a review. Ann For Sci 66:602–602. doi:0.1051/forest/2009041

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Benis EN, Paracchini ML, Zulian G, Schägner JP, Bidoglio G (2014) Exploring restoration options for habitats, species and ecosystem services in the European Union. J Appl Ecol 51:899–908. doi: 10.1111/1365-2664.12251

Bergès L, Feiss T, Avon C, Martin H, Rochel X, Dauffy-Richard E, Cordonnier T, Dupouey J (2017) Response of understorey plant communities and traits to past land use and coniferous plantation. Appl Veg Sci 20:468–481. doi: 10.1111/avsc.12296

Bradshaw RH, Jones CS, Edwards SJ, Hannon GE (2015) Forest continuity and conservation value in Western Europe. The Holocene 25:194–202. doi: 10.1177/0959683614556378

Brown ND, Curtis T, Adams EC (2015) Effects of clear-felling versus gradual removal of conifer trees on the survival of understorey plants during the restoration of ancient woodlands. For Ecol Manag 348:15–22. doi: 10.1016/j.foreco.2015.03.030

Canty, A. and Ripley, B. (Bradshaw). (2017) boot: Bootstrap R (S-Plus) Functions. R package version 1.3-20.

Convention on Biological Diversity (2001) Report of the ad hoc technical expert group on Forest Biological Diversity. Subsidiary body on scientific, technical and technological advice.

Coppins AM, Coppins BJ (2002) Indices of ecological continuity for woodland epiphytic lichen habitats in the British Isles. British Lichen Society London.

Coppins BJ, Coppins AM (2005) Lichens — the biodiversity value of western woodlands. Bot J Scotl 57:141–153. doi: 10.1080/03746600508685093

Curt T, Prévosto B, Klesczewski M, Lepart J (2003) Post-grazing scots pine colonization of midelevation heathlands: population structure, impact on vegetation composition and diversity. Ann. For. Res. 60: 711–24. doi: 10.1051/forest:2003065

Davison AC, Hinkley DV (1997) Bootstrap methods and their applications. Cambridge Universit y Press, Cambridge. ISBN 0-521-57391-2

Douda J, Boubl K, Doudov J, Michal Kyncl M (2017) Traditional forest management practices stop forest succession and bring back rare plant species. J. Appl. Ecol. 54:761–71. doi:10.1111/1365-2664.12801.

Dray S, Dufour A (2007) The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22: 1-20.

Ellenberg H, Weber HE, Düll R (1992) Zeigerwerte von Pflanzen in Mitteleuropa. Verlag Wrich Goltze

Ellis CJ (2012) Lichen epiphyte diversity: A species, community and trait-based review. Perspect Plant Ecol Evol Syst 14:131–152. doi: 10.1016/j.ppees.2011.10.001

European Union Habitats Directive Annex I https://ec.europa.eu/environment/nature/legislation/habitatsdirectiveEuropean Union, Accessed June 2017.

FAO (2016) State of the World's Forests 2016. Forests and agriculture: land-use challenges and opportunities. Rome.

Ferris R, Peace AJ, Humphrey JW, Broome AC (2000) Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. For Ecol Manag 136:35–51. doi: 10.1016/S03781127(99)00268-6

Forestry Commission (2013) Forestry Statistics 2013: A compendium of statistics about woodland, forestry and primary wood processing in the United Kingdom. Forestry Commission, Edinburgh.https://forestresearch.gov.uk/tools-and-resources/statistics. Accessed June 2017.

Forestry Commission (2017) *The UK Forestry Standard (Fourth Edition)*, Edinburgh.

Fukami T, Bezemer M, Mortimer SR, van der Putten WH (2005) Species divergence and trait convergence in experimental plant community assembly. Ecol. Lett. 8:1283–90. doi:10.1111/j.1461-0248.2005.00829.x.

Gaio-Oliveira G, Dahlman L, Máguas C, Palmqvist K (2004) Growth in relation to microclimatic conditions and physiological characteristics of four Lobaria pulmonaria populations in two contrasting habitats. Ecography 27:13–28. doi: 10.1111/j.0906-7590.2004.03577.x

Gardiner BA, Quine CP (2000) Management of forests to reduce the risk of abiotic damage – a review with particular reference to the effects of strong winds. For Ecol Manag 135:261–277

Gauslaa Y, Bartemucci P, Solhaug KA (2019) Forest edge-induced damage of cephalo- and cyanolichens in northern temperate rainforests of British Columbia. Can J Forest Res 49: 434-439. https://doi.org/10.1139/cjfr-2018-0187

Gauslaa Y, Solhaug KA (1999) High-light damage in air-dry thalli of the old forest lichen *Lobaria pulmonaria*—interactions of irradiance, exposure duration and high temperature. J Exp Bot 50:

697–705. doi:10.1093/jxb/50.334.697

Gauslaa Y, Solhaug KA (1996) Differences in the Susceptibility to Light Stress Between Epiphytic Lichens of Ancient and Young Boreal Forest Stands. Funct Ecol 10:344–354. doi: 10.2307/2390282

Green TGA, Lange OL (1995) Photosynthesis in Poikilohydric Plants: A Comparison of Lichens and Bryophytes. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of Photosynthesis. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 319–341

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. doi: 10.1086/283244

Grime JP, Hodgson JG, Hunt R (2007) Comparative Plant Ecology: A comparative approach to common British Species. Castlepoint Press, Kirkcudbrightshire.

Harmer R, Boswell R, Robertson M (2005) Survival and growth of tree seedlings in relation to changes in the ground flora during natural regeneration of an oak shelterwood. For Int J For Res 78:21–32. doi: 10.1093/forestry/cpi003

Harmer R, Kerr G, Thompson R (2010) Managing native broadleaved woodland. The Stationery Office Ltd, Edinburgh

Hill MO (1999) Ellenberg's indicator values for British plants. Center for Ecology and Hydrology, Natural Environment research Council, Abbots Ripton, Huntingdon

Humphrey JW, Davey S, Peace AJ, 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. Biol Conserv 107:165–180. doi: 10.1016/S0006-3207(02)00057-5

Hunt R, Hodgson JG, Thompson K, Bungener P, Dunnett NP, Askew AP (2004) A new practical tool for deriving a functional signature for herbaceous vegetation. Appl. Veg. Sci. 7: 163–170. doi:10.1111/j.1654-109X.2004.tb00607.x.

James PW, Hawksworth DL, Rose F (1977) Lichen communities in the British Isles: a preliminary conspectus. In: Academic Press. London

Jüriado I, Liira J, Paal J, Suija A (2008) Tree and stand level variables influencing diversity of lichens on temperate broad-leaved trees in boreo-nemoral floodplain forests. Biodivers Conserv 18:105. doi:10.1007/s10531-008-9460-y

Joint Nature Conservation Committee (JNCC) Annex I Habitat accounts. https://jncc.defra.gov.uk/protectedsites/sacselection/habitat.asp?FeatureIntCode=H91A0. Accessed July 2017

Kirby KJ (1988) Changes in the ground flora under plantations on ancient woodland sites. *Forestry*, 61:317–338.

Kirby KJ, Goldberg EA, Orchard N (2017) Long-term changes in the flora of oak forests and of oak:spruce mixtures following removal of conifers. For Int J For Res 90:136–147. doi:10.1093/forestry/cpw049

Knapp BO, Walker JL, Wang GG, Hu H, Addington RN (2014) Effects of overstory retention, herbicides, and fertilization on sub-canopy vegetation structure and functional group composition in loblolly pine forests restored to longleaf pine. For Ecol Manag 320:149–160. doi: 10.1016/j.foreco.2014.03.021

Kolk J, Naaf T (2015) Herb layer extinction debt in highly fragmented temperate forests - completely paid after 160 years? Biol. Conserv.182:164–72. doi:10.1016/j.biocon.2014.12.004.

Kolk J, Naaf T, Wulf M (2017) Paying the colonization credit: converging plant species richness in ancient and post-agricultural forests in NE Germany over five decades. Biodivers. Conserv. 26: 735–55. doi:10.1007/s10531-016-1271-y.

Legendre P, Galzin R, Harmelin-Vivien ML (1997) Relating behavior to habitat: solutions to the fourth-corner problem. Ecology 78: 547-562.

Leppik E, Jüriado I, Liira J (2011) Changes in stand structure due to the cessation of traditional land use in wooded meadows impoverish epiphytic lichen communities. The Lichenologist 43:257–274.doi: 10.1017/S002428291100003X

MacKenzie TD, MacDonald TM, Dubois LA, Campbell DA (2001) Seasonal changes in temperature and light drive acclimation of photosynthetic physiology and macromolecular content in *Lobaria pulmonaria*. Planta, 214(1):57-66.

Naaf T, Kolk J (2015) Colonization credit of post-agricultural forest patches in NE Germany remains 130-230 years after reforestation. Biol. Conserv. 182: 155–63. doi:10.1016/j.biocon.2014.12.002.

Nordén, B., Dahlberg, A., Brandrud, T.E., Fritz, Ö., Ejrnaes, R., Ovaskainen, O., 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Ecoscience 21, 34–45. https://doi.org/10.2980/21-1-3667.

Palmer SCF, Mitchell R J, Truscott AM, Welch D (2005) Regeneration in Atlantic oakwoods : has deer management had a beneficial effect ? Regeneration in Atlantic Oakwoods : Botanical Journal of Scotland, 57:167–178.

Palmqvist K, Sundberg B (2000) Light use efficiency of dry matter gain in five macro-lichens: relative impact of microclimate conditions and species-specific traits. Plant Cell Environ 23:1–14. doi:10.1046/j.1365-3040.2000.00529.x

Patterson G, Nelson D, Robertson P, Tullis J (2014) Scotland's native woodlands results from the Native Woodland Survey of Scotland. Forestry Commission Scotland, Edinburgh, UK.

Paul TSH, Ledgard NJ (2009) Vegetation succession associated with wilding conifer removal. New Zealand Plant Protection 62:374-379.

Pfestorf H, Weiß L, Müller J, Boch S, Socher SA, Prati D, Schöning I, Weisser W, Fischer M, Jeltsch F (2013) Community mean traits as additional indicators to monitor effects of land-use intensity ongrassland plant diversity. Perspect Plant Ecol Evol Syst 15:1–11. doi: 10.1016/j.ppees.2012.10.003

Polley HW, Derner JD, Wilsey BJ (2005) Patterns of plant species diversity in remnant and restored tallgrass prairies. Restor Ecol 13:480–487. doi: 10.1111/j.1526-100X.2005.00060.x

Pryor SN, Curtis TA, Peterkin GF (2002) Restoring plantations on ancient woodland sites. The

Woodland Trust, Grantham, UK.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rackham, O (1989) The last forest: story of Hatfield Forest. J.M. Dent & Sons Ltd., London.

Reemts CM, Eidson JA (2019) Choosing plant diversity metrics: a tallgrass prairie case study. Ecological Restoration 37: 233–45. doi:10.3368/er.37.4.233.

Renhorn K-E, Esseen P-A, Palmqvist K, Sundberg B (1996) Growth and vitality of epiphytic lichens. Oecologia 109:1–9. doi: 10.1007/s004420050051

Rodwell JS (2005) Woodlands at the edge : A European perspective on the Atlantic Oakwood plant communities. Botanical Journal of Scotland 57: 121–133

Rodwell JS, Patterson GS (1994) Creating new native woodlands. HMSO, London

SER: Society for Ecological Restoration Science and Policy Working Group (2004) The SER international primer on ecological restoration

Scottish Natural Heritage (2011) A guide to understanding the Scottish Ancient Woodland Inventory (AWI). https://www.nature.scot/guide-understanding-scottish-ancient-woodland-inventory-awi Accessed January 2021.

Shackelford N, Hobbs RJ, Burgar JM, Erickson TE, Fontaine JB, Laliberté E, Ramalho CE, Perring MP, Standish RJ (2013) Primed for change: developing ecological restoration for the 21st Century.Restor Ecol 21:297–304. doi: 10.1111/rec.12012

Thompson RN, Hope JCE (2005) Restoring planted ancient woodland sites — assessment, silviculture and monitoring. Bot J Scotl 57:211–227. doi: 10.1080/03746600508685099

van Kooten O, Snel JFH (1990) The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth Res 25:147–150. doi: 10.1007/BF00033156

Verheyen K, Bossuyt B, Hermy M, Tack G (1999) The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. J Biogeogr 26:1115–1128

Watts K, Whytock RC, Park JK, Fuentes-Montemayor, E, Macgregor,NA, Duffield S, McGowan PJK (2020) Ecological time lags and the journey towards conservation success. Nat Ecol Evol 4: 304-311 https://doi.org/10.1038/s41559-019-1087-8

Wickham, H (2016) ggplot2: Elegant graphics for data analysis. 2nd Edition. Springer-Verlag New York. doi:10.1007/978-3-319-24277-4

Young TP (2000) Restoration ecology and conservation biology. Biol Conserv 92:73–83. doi:10.1016/S0006-3207(99)00057-9

g. Tables

Table 1: Mean number of species (ground flora and tree seedlings/saplings) in each quadrant in 2008 and 2016 and p-values for paired t-test. SD = standard deviation

Quadrat location	Mean No. of Species 2008	SD 2008	Mean No. of Species 2016	SD 2016	p value
Within remnant:					
6 m from remnant boundary (Q0)	5.17	2.38	6.56	1.72	0.054
Within former plantation:					
3 m from remnant boundary (Q9)	3.67	2.30	6.67	2.03	<0.0001
6 m from remnant boundary (Q12)	3.33	1.61	6.00	1.75	0.00027
9 m from remnant boundary (Q15)	3.06	1.63	6.50	1.86	0.00049

Table 2: Change in cover (cm^2) for each species of lichen between 2007 and 2016 in each of the patches photographed (cm^2 area rounded to nearest unit), in *remnants* and in *ASNW*. Blank cells indicate lichen species was absent in both 2007 and 2016 from the sampled patches, (o) = lichen species which disappear i.e. present in 2007 and completely absent in 2016 from the sampled patches; (*) = lichens which appear i.e. absent in 2007 and present in 2016 in the sampled patches. 1 patch photographed in 0.02 m^2 frame, 2 patches photographed in 0.04 m^2 frame.

	Patch id	*Squamules of Cladonia spp*	*Degelia atlantica*	*Hypotrachyna sinuosa*	*Ochrolechia androgyna*	*Platismatia glauca*	*Lobaria pulmonaria*	*Lobaria scrobiculata*	*Stricta limbata*	*Lichenoconium usneae*	*Lobaria virens*
Remnant	**1**[1]	*6									-75
	2[1]										°-130
	5[1]										57
	7[2]										39
	8[2]										87
	15[2]						-179	°-4		°-3	85
	17[2]	*4	*89				117	°-14			°-28
	18[1]	*23									°-82
	19[2]	-4					°-76		°-3		*31
	20[2]	*12	°-85		°-31		-17	*26			
	21[2]						°-24	-4			

	22[2]		22				49				
	39[2]				°-19	°-42	64				
	40[2]	°-2					-154				
ASNW	**29**[2]						172				
	30[2]						<1				
	31[2]			-32	°-3	*50	-45				
	32[1]						<1			<1	
	33[2]	°-3			°-2						-33
	34[2]	°-14					99				
	35[2]				*11	°-12	°-4				29
	36[2]	8			*10		°-1				18

h. Captions for figures

Fig 1: (a) Geographic location of Glencripesdale planted ancient woodland site and of the nine other Scottish oak woodlands to which its climatic data was compared (Fig. 1 and Table 1, Appendix A in supplementary material). Grade of *Index of Ecological Continuity* (*IEC*) influencing lichen community composition is represented by symbols: dots for *Western Scotland IEC,* squares for *Eastern Scotland IEC,* triangles for *NEW IEC. (b)* Arrangement of Ancient Semi Natural Woodland (*ASNW*), conifer *plantation* areas (felled in image) and embedded ASNW *remnants* (also showing vegetation plot layout-plots extend from the ASNW *remnants* in to the *plantation*) within Glencripesdale study site.

Fig 2: Relationship between plant traits (C- competitor, R – ruderal, S – stress tolerator Grime strategies, and Ellenberg values for light, moisture and nitrogen) and environment (location *former plantation*, *remnants* by year 2008, 2016).

Fig. 3: Chlorophyll fluorescence yields as an indicator of lichen vitality measured from thalli of *Lobaria pulmonaria* (LP) and *L. virens* (LV) growing on *remnant* trees (n=14 LP thalli, n= 18 LV thalli) and *ASNW* trees (n=10 LP thalli, n= 10 LV thalli) at three time-points (1= autumn prior to removal of conifer plantation, 2= autumn in year following conifer plantation removal, 3 = autumn 9 years after conifer plantation removal). Significant differences ($p<0.05$) in CF yield from thalli on *remnant* trees compared to *ASNW* trees are shown by independent t-tests (* = Welch's t-test performed due to heterogeneity in variance) for LP at time point 1 (t = 3.000, df =22, P = 0.008*), 2 (t = 15.200, df = 22, P = <0.0001*) and 3 (t = -1.050, df = 22, P = 0.304), and for LV at time point 2 (t = 6.880, df = 26, P = <0.0001*) and 3 (t = 0.902, df = 26, P = 0.375).

Fig. 4: Bootstrapped confidence intervals (95%) for mean change in epiphytic lichen cover (cm^2) between 2007 and 2016 in the patches sampled on *ASNW* and *remnants* trees, estimated with 5000 resamples.

i. figures

(a) (b)

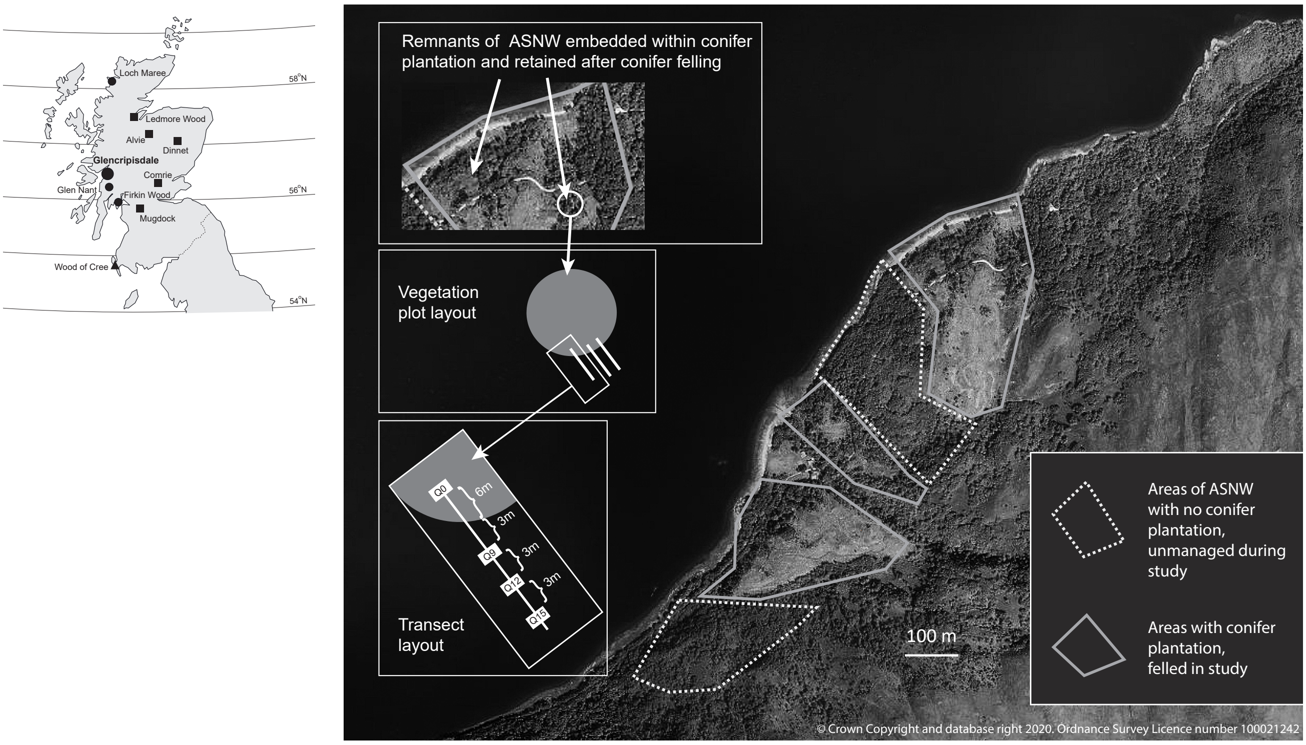

Fig 1: (a) Geographic location of Glencripesdale planted ancient woodland site and of the nine other Scottish oak woodlands to which its climatic data was compared (Fig. 1and Table 1, Appendix A in supplementary material). Grade of *Index of Ecological Continuity* (*IEC*) influencing lichen community composition is represented by symbols: dots for *Western Scotland IEC,* squares for *Eastern Scotland IEC,* triangles for *NEW IEC. (b)* Arrangement of Ancient Semi Natural Woodland (*ASNW*), conifer *plantation* areas (felled in image) and embedded ASNW *remnants* (also showing vegetation plot layout- plots extend from the ASNW *remnants* in to the *plantation*) within Glencripesdale study site.

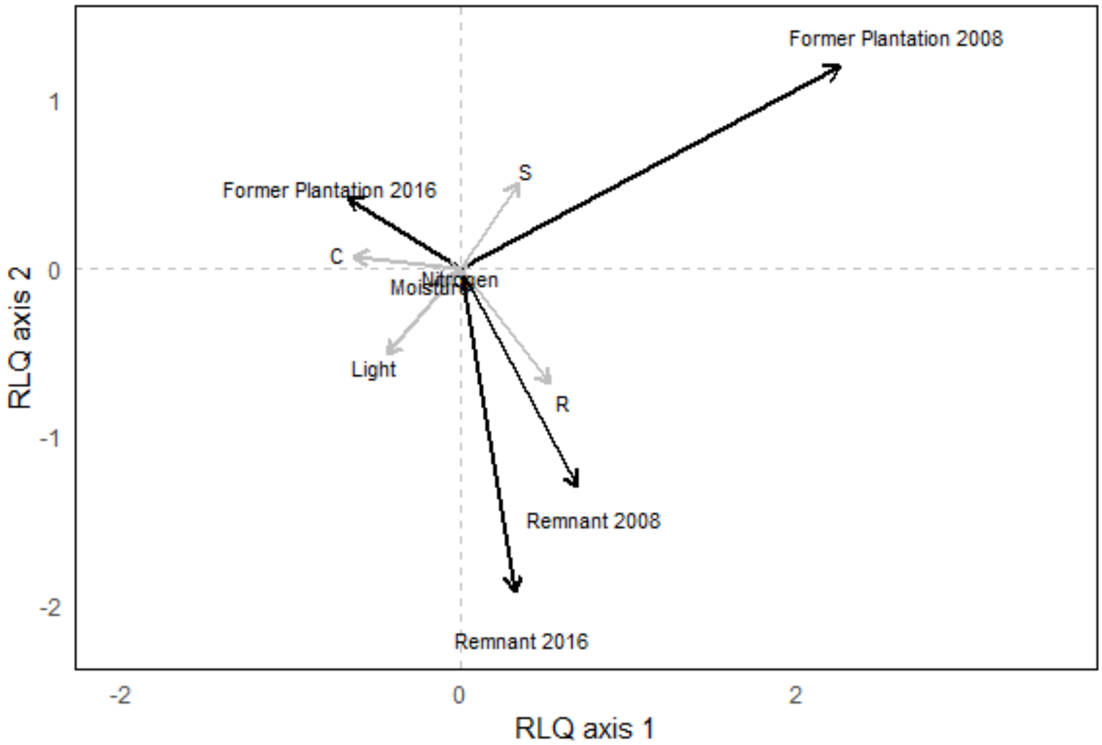

Fig 2: Relationship between plant traits (C- competitor, R – ruderal, S – stress tolerator Grime strategies, and Ellenberg values for light, moisture and nitrogen) and environment (location *former plantation*, *remnants* by year 2008, 2016).

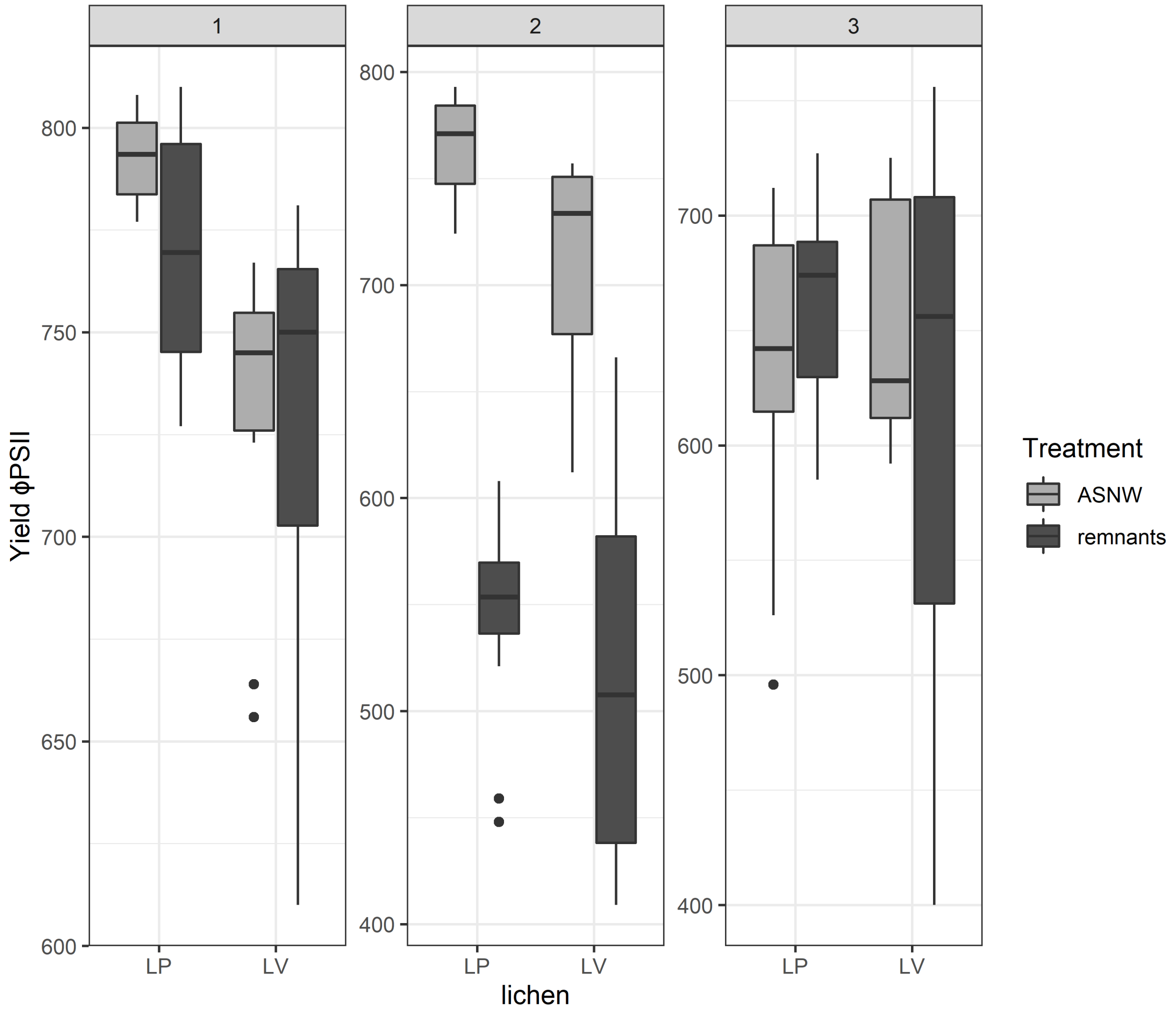

Fig. 3: Chlorophyll fluorescence yields as an indicator of lichen vitality measured from thalli of *Lobaria pulmonaria* (LP) and *L. virens* (LV) growing on *remnant* trees (n=14 LP thalli, n= 18 LV thalli) and *ASNW* trees (n=10 LP thalli, n= 10 LV thalli) at three time-points (1= autumn prior to removal of conifer plantation, 2= autumn in year following conifer plantation removal, 3 = autumn 9 years after conifer plantation removal). Significant differences ($p<0.05$) in CF yield from thalli on *remnant* trees compared to *ASNW* trees are shown by independent t-tests (* = Welch's t-test performed due to heterogeneity in variance) for LP at time point 1 (t = 3.000, df =22, P = 0.008*), 2 (t = 15.200, df = 22, P = <0.0001*) and 3 (t = -1.050, df = 22, P = 0.304), and for LV at time point 2 (t = 6.880, df = 26, P = <0.0001*) and 3 (t = 0.902, df = 26, P = 0.375).

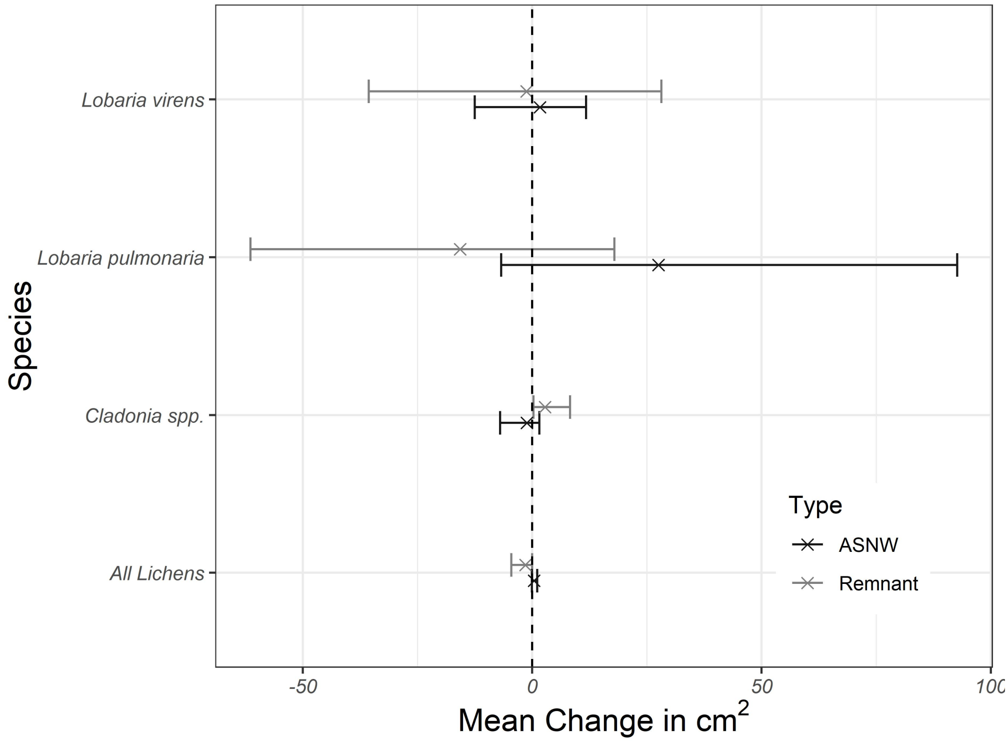

Fig. 4: Bootstrapped confidence intervals (95%) for mean change in epiphytic lichen cover (cm^2) between 2007 and 2016 in the patches sampled on *ASNW* and *remnants* trees, estimated with 5000 resamples.