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RESEARCH PAPER

# 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-ha 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.

**Keywords** ASNW · PAWS · Restoration · Lichen · Conservation · Species traits

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## 1 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* (oak) and *Fagus* (beech) of western Europe, and un-fragmented ASNWs in Scotland have often been managed for centuries (Scottish Natural Heritage 2011; Verheyen et al. 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 Naaf 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' (European Commission 2018; JNCC 2019). "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.

## 2 Materials and methods

### 2.1 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 ha at elevations of less than 60 m above sea level. The PAWS consists of two types of woodland: firstly, fragments (> 2 ha in size) of ancient semi-natural woodland (hereafter referred to as *ASNW*) and secondly, areas of conifer plantation comprised of Sitka spruce (*Picea sitchensis*), 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 referred 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 (Appendix Fig. 5) 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 Appendix Table 3 for details).

The objectives of the restoration treatments were 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.

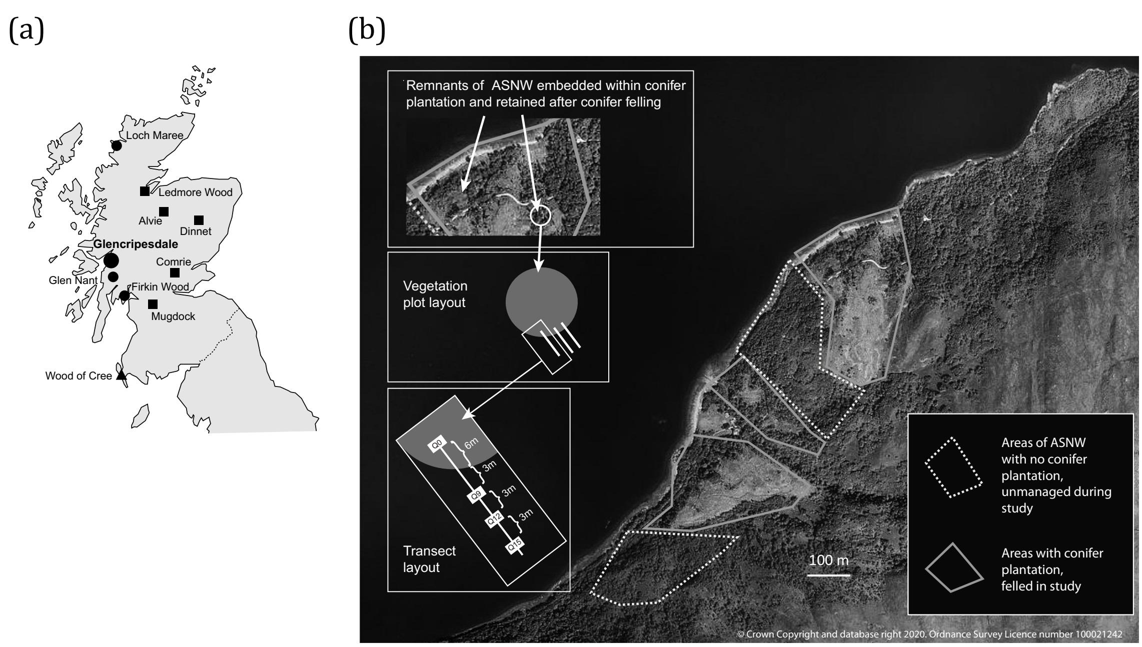


**Fig. 1** **a** Geographic location of Glencripesdale planted ancient woodland site and of the nine other Scottish oak woodlands to which its climatic data was compared (Appendix Fig. 5 and Table 3). Grade of *Index of Ecological Continuity* (*IEC*) influencing lichen community composition is represented 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

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.

## 2.2 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 (3 m apart, 15 m long) running from the *remnant* into the *former plantation*, with four quadrats (0.5 m × 0.5 m) positioned along each. The first quadrat (Q0) was positioned inside the *remnant* at 6 m from the *former plantation* boundary (ecotone), and the remaining 3 quadrats inside the *former plantation* at 3 m (Q9), 6 m (Q12) and 9 m (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.

## 2.3 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 Appendix.

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 *Western Scotland Index of Ecological Continuity* and the *New Index of Ecological Continuity*

(Coppins and Coppins 2002) (Appendix Table 4). 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 these 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 0.04-$m^2$ frame was fixed around each patch with three plastic nails set into the bark; for smaller lichen patches, a half-frame measuring 0.02 $m^2$ was used. The sample patches were located at surveyor height (between 52 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.

## 3 Data analysis

### 3.1 Evaluating restoration success through ground flora species colonization and trait composition

#### 3.1.1 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 et al. 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.

#### 3.1.2 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

**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 |

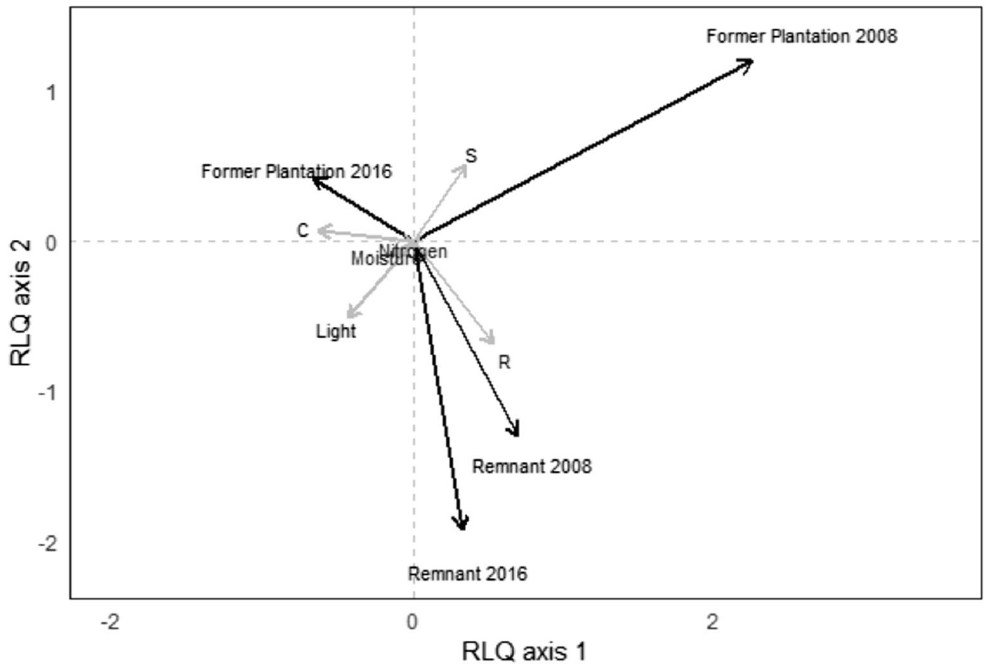


**Fig. 2** Relationship between plant traits (C- competitor, R – ruderal, S – stress tolerator Grime strategies, and Ellenberg values for light, moisture and nitrogen) and environment (location *former plantation*, *remnants* by year 2008, 2016)

*remnants,* with species requiring/utilising 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

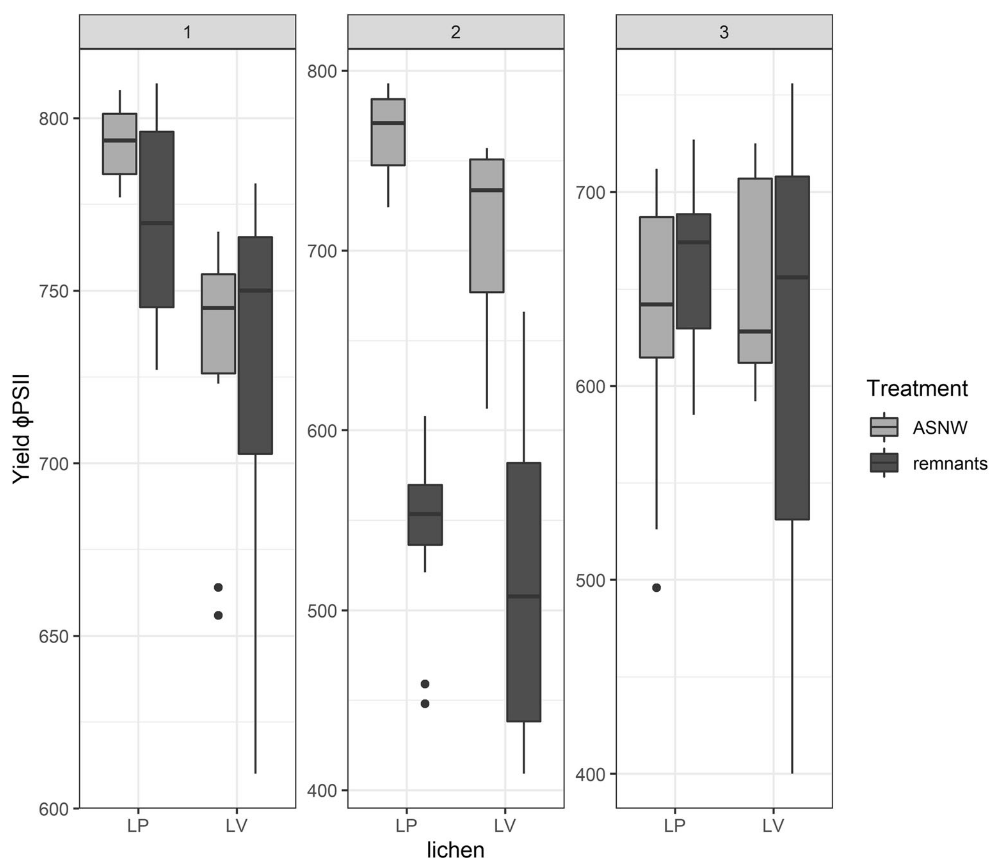


**Fig. 3** Chlorophyll fluorescence yields as an indicator of lichen vitality measured from thalli of *Lobaria pulmonaria* (LP) and *L. virens* (LV) growing on *remnant* trees (n = 14 LP thalli, n = 18 LV thalli) and *ASNW* trees (n = 10 LP thalli, n = 10 LV thalli) at three time-points (1 = autumn prior 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 ($t = 15.200$, $df = 22$, $P = < 0.0001$*) but not 3 ($t = -1.050$, $df = 22$, $P = 0.304$), and for LV at time point 2 ($t = 6.880$, $df = 26$, $P = < 0.0001$*) but not 1 ($t = 0.088$, $df = 26$, $P = 0.931$) or 3 ($t = 0.902$, $df = 26$, $P = 0.375$)

**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; (–) = decline in cover of lichen between 2007 and 2016; (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 |

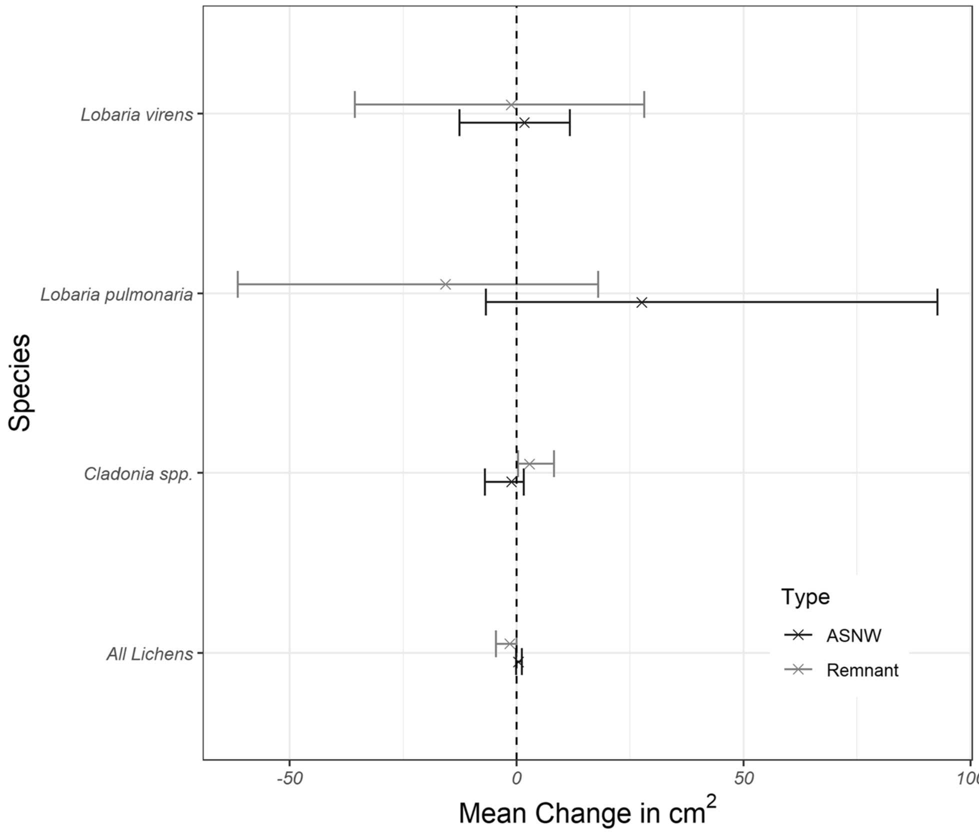


**Fig. 4** Bootstrapped confidence intervals (95%) for mean change in epiphytic lichen cover ($cm^2$) between 2007 and 2016 in the patches sampled on *ASNW* and *remnants* trees, estimated with 5000 resamples

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

**Table 3** Values and standard errors of continentality (°C), heat moisture index and yearly growing degrees (sum of degrees above 5 °C), calculated on climatic data ranging from 2007 to 2016 for 10 Scottish oak woodland sites including our study site, Glencripesdale (shown in bold). The letters indicate groups of mean values that differ at a 5% level determined by Tukey's post hoc test

| Oak Woodland | Met Station | Continentality (°C) | Yearly growing degrees (°C) | Annual heat: moisture index |
|---|---|---|---|---|
| **Glencripesdale** | **Dunstaffnage** | **10.9a (± 0.7)** | **1775bc (± 100)** | **12c (± 0.8)** |
| Loch Maree | Poolewe | 11.2a (± 0.8) | 1437ab (± 100) | 11.9c (± 0.8) |
| Alvie | Aviemore | 13.2a (± 0.6) | 1331ab (± 100) | 18.3de (± 0.8) |
| Dinnet | Aboyne | 13.2a (± 0.6) | 1331ab (± 100) | 22.1f (± 0.8) |
| Comrie | Drummond Castle | 12.3a (± 0.8) | 1025a (± 100) | 14.8cd (± 0.8) |
| Firkin wood | Benmore | 12a (± 0.7) | 1631bc (± 100) | 7.1a (± 0.8) |
| Mugdock | Mugdock Park | 12.8a (± 0.8) | 1091a (± 100) | 11.3bc (± 0.8) |
| Wood of Cree | Portpatrick | 10.6a (± 0.8) | 1931c (± 112) | 19.2ef (± 0.9) |
| Glen Nant | Inverinan Beg | 12.8a (± 0.8) | 1464abc (± 112) | 7.6ab (± 0.9) |
| Ledmore Wood | Urquhart | 11.9a (± 1.1) | 1379abc (± 159) | 22.5ef (± 1.2) |

**Table 4** Epiphytic lichen species identified from a site inventory conducted in 2005 at Glencripesdale and their *Index of Ecological Continuity* (*IEC*) status to inform the identification of lichen indicator community patches monitored during this study and species' conservatism score (see Reemts and Eidson 2019)

| | Instances in *remnants* | Instances in *ASNW* | Substrates | IEC Status | Conservatism coefficient (1 low–10 high) |
|---|---|---|---|---|---|
| Lichens | | | | | |
| Degelia atlantica | 3 | 2 | C,Q | R | 4 |
| Degelia plumbea | 2 | 2 | C,Fx,Q | R | 4 |
| Dimerella lutea | 1 | – | B | R | 4 |
| Hypotrachyna sinuosa | 2 | 1 | B | Eu | 7 |
| Hypotrachyna taylorensis | – | 1 | B | Eu,WS | 9 |
| Lobaria amplissima | 1 | – | Q | R,WS | 9 |
| Lobaria pulmonaria | 5 | 5 | Al,B,C,Fx,Q | R | 4 |
| Lobaria scrobiculata | 7 | – | B,C,Q | R,WS | 9 |
| Lobaria virens | 15 | 4 | B,C,Fx,Q | R | 4 |
| Menegazzia terebrata | 5 | 1 | B | Eu | 7 |
| Nephroma laevigatum | 2 | – | C,Fx | R | 4 |
| Pannaria conoplea | – | 2 | C,Q | R | 4 |
| Pannaria rubiginosa | 1 | 1 | C,Q | | 3 |
| Parmeliella parvula | 1 | 1 | B | | 3 |
| Parmotrema crinitum | 1 | 1 | B | R | 4 |
| Peltigera collina | 1 | 1 | C,Q | R,WS | 9 |
| Sticta fuliginosa* | 5 | 2 | C,B,Q | R | 4 |
| Sticta limbata | 2 | 2 | C | R | 4 |
| Sticta sylvatica* | 5 | 1 | C,Fx,Q | R | 4 |
| Thelotrema lepadinum | 1 | 2 | Q | R | 4 |
| Additional lichen species encountered in the 2007 and 2016 survey of the sample patches | | | | | |
| Squamules of *Cladonia* spp | | | *Cladonia luteoalba* has EU | | 4 |
| *Ochrolechia androgyna* | | | | | 0 |
| *Platismatia glauca* | | | | | 0 |
| *Lichenoconium usneae* | | | | | 0 |

Abbreviations: Al = Alnus, B= Betula, C = Corylus. Fx= Fraxinus, Q = Quercus; Eu = Eu-*Oceanic Calcifuge Woodland Index of Ecological Continuity*, WS = *WesternScotland Index of Ecological Continuity*, R = *The Revised Index of Ecological Continuity* (Coppins & Coppins, 2002). The two, asterisked species are difficult to distinguish when immature, so confusion between these two taxa is possible. WS species are indicators for ancient deciduous woodlands and have the highest fidelity for Atlantic oakwoods, and these species are given the highest conservatism coefficient (9), Eu species are indicators for upland woodlands with oceanic climates, there is overlap in habitat with WS, they have been allocated a conservatism coefficient of 7. R species are strongly associated with ancient woodlands however these species may show lower fidelity in Western Scotland (Thompson and Hope 2005) so have been allocated a lower conservatism coefficent (4). A species may be allocated more than one conservatism coefficient, but the maximum value conservatism coefficient is attributed in calculation of the diversity metric

revised Ellenberg values for British plants (Hill 1999) for light, moisture and nitrogen. Grime strategies (Grime et al. 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 and Dufour 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 (Appendix Table 5). 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.

**Table 5** Species trait values used for creation of Q matrix: the Grime C-S-R strategies (Hunt et al. 2004) and Ellenberg light, moisture and nitrogen values (Hill 1999) for the 53 species available

| | Light | Moisture | Nitrogen | C | S | R |
|---|---|---|---|---|---|---|
| Agrostis capillaris | 6 | 5 | 4 | 0.333 | 0.333 | 0.333 |
| Agrostis stolonifera | 7 | 6 | 6 | 0.500 | 0.000 | 0.500 |
| Agrostis vinealis | 7 | 6 | 2 | 0.333 | 0.333 | 0.333 |
| Ajuga reptans | 5 | 7 | 5 | 0.167 | 0.167 | 0.667 |
| Alnus glutinosa | 5 | 8 | 6 | 0.500 | 0.500 | 0.000 |
| Anthoxanthum odoratum | 7 | 6 | 3 | 0.167 | 0.417 | 0.417 |
| Betula pendula | 7 | 5 | 4 | 0.750 | 0.250 | 0.000 |
| Betula pubescens | 7 | 7 | 4 | 0.750 | 0.250 | 0.000 |
| Blechnum spicant | 5 | 6 | 3 | 0.167 | 0.667 | 0.167 |
| Calluna vulgaris | 7 | 6 | 2 | 0.250 | 0.750 | 0.000 |
| Cardamine flexuosa | 5 | 7 | 6 | 0.000 | 0.250 | 0.750 |
| Cardamine hirsuta | 8 | 5 | 6 | 0.000 | 0.500 | 0.500 |
| Carex spicata | 7 | 6 | 4 | 0.333 | 0.333 | 0.333 |
| Chrysosplenium oppositifolium | 5 | 9 | 5 | 0.417 | 0.167 | 0.417 |
| Cirsium palustre | 7 | 8 | 4 | 0.417 | 0.167 | 0.417 |
| Corylus avellana | 4 | 5 | 6 | 0.500 | 0.500 | 0.000 |
| Deschampsia cespitosa | 6 | 6 | 4 | 0.417 | 0.417 | 0.167 |
| Deschampsia flexuosa | 6 | 5 | 3 | 0.250 | 0.750 | 0.000 |
| Digitalis purpurea | 6 | 6 | 5 | 0.167 | 0.417 | 0.417 |
| Dryopteris dilatata | 5 | 6 | 5 | 0.417 | 0.417 | 0.167 |
| Dryopteris filix-mas | 5 | 6 | 5 | 0.500 | 0.500 | 0.000 |
| Epilobium brunnescens | 7 | 8 | 3 | 0.167 | 0.167 | 0.667 |
| Epilobium palustre | 7 | 8 | 3 | 0.167 | 0.667 | 0.167 |
| Galium saxatile | 6 | 6 | 3 | 0.167 | 0.667 | 0.167 |
| Geranium robertianum | 5 | 6 | 6 | 0.167 | 0.167 | 0.667 |
| Geum urbanum | 4 | 6 | 7 | 0.417 | 0.167 | 0.417 |
| Holcus lanatus | 7 | 6 | 5 | 0.333 | 0.333 | 0.333 |
| Holcus mollis | 6 | 6 | 3 | 0.667 | 0.167 | 0.167 |
| Hyacinthoides non-scripta | 5 | 5 | 6 | 0.000 | 0.500 | 0.500 |
| Hypericum perforatum | 7 | 4 | 5 | 0.417 | 0.167 | 0.417 |
| Ilex aquifolium | 5 | 5 | 5 | 0.500 | 0.500 | 0.000 |
| Juncus bulbosus | 7 | 10 | 2 | 0.000 | 0.750 | 0.250 |
| Juncus effusus | 7 | 7 | 4 | 0.750 | 0.250 | 0.000 |
| Luzula multiflora | 7 | 6 | 3 | 0.167 | 0.667 | 0.167 |
| Lysimachia nemorum | 5 | 7 | 5 | 0.167 | 0.167 | 0.667 |
| Molinia caerulea | 7 | 8 | 2 | 0.500 | 0.500 | 0.000 |
| Oxalis acetosella | 4 | 6 | 4 | 0.000 | 0.750 | 0.250 |
| Phalaris arundinacea | 7 | 8 | 7 | 1.000 | 0.000 | 0.000 |
| Poa trivialis | 7 | 6 | 6 | 0.167 | 0.167 | 0.667 |
| Potentilla erecta | 7 | 7 | 2 | 0.167 | 0.667 | 0.167 |
| Primula vulgaris | 5 | 5 | 4 | 0.167 | 0.667 | 0.167 |
| Prunella vulgaris | 7 | 5 | 4 | 0.333 | 0.333 | 0.333 |
| Pteridium aquilinum | 6 | 5 | 3 | 1.000 | 0.000 | 0.000 |
| Quercus petraea | 6 | 6 | 4 | 0.500 | 0.500 | 0.000 |
| Ranunculus flammula | 7 | 9 | 3 | 0.417 | 0.167 | 0.417 |
| Ranunculus repens | 6 | 7 | 7 | 0.500 | 0.000 | 0.500 |
| Rubus fruticosus | 6 | 6 | 6 | 0.500 | 0.500 | 0.000 |
| Rubus idaeus | 6 | 5 | 5 | 0.500 | 0.500 | 0.000 |

**Table 5** (continued)

| | Light | Moisture | Nitrogen | C | S | R |
|---|---|---|---|---|---|---|
| Senecio jacobaea | 7 | 4 | 4 | 0.417 | 0.167 | 0.417 |
| Stachys sylvatica | 6 | 6 | 8 | 0.750 | 0.000 | 0.250 |
| Veronica chamaedrys | 6 | 5 | 5 | 0.333 | 0.333 | 0.333 |
| Viola palustris | 7 | 9 | 2 | 0.167 | 0.417 | 0.417 |
| Viola riviniana | 6 | 5 | 4 | 0.167 | 0.667 | 0.167 |

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.

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

### 3.2.1 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* in *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).

### 3.2.2 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

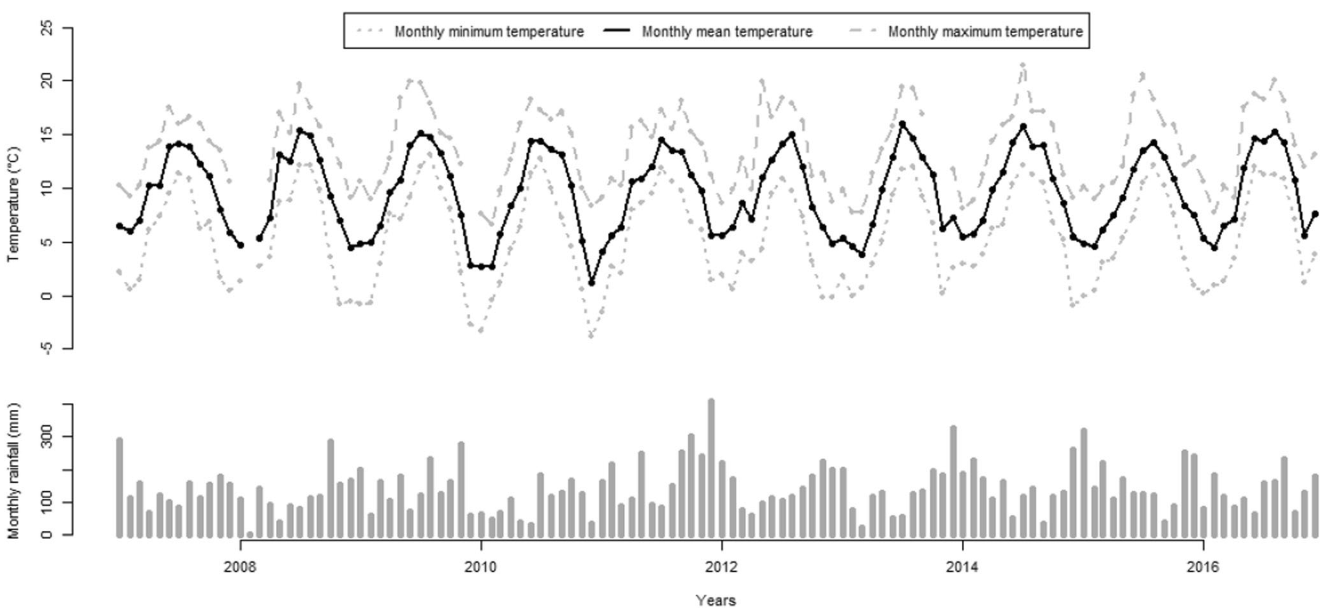


**Fig. 5** Minimum, mean and maximum monthly temperatures and total monthly precipitations for the Glencripesdale site (Dunstaffnage met station) from 2007 to 2016 covering the years of the PAWS restoration study from pre-conifer removal to nine years after conifer removal

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 (Canty 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) (Appendix Table 4). 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).

## 4 Results

### 4.1 Evaluation of change in ground vegetation and trait composition

#### 4.1.1 Ground flora species richness

There was a significant increase in species richness of the ground flora between 2008 and 2016 in the *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*.

#### 4.1.2 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.

#### 4.1.3 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 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 colonized a different sample area, e.g. from *remnants* to *former plantation*. *Indicator* species count increased significantly from 2008 to 2016 in the *former plantation* ($\beta$ =1.375, Std. Error = 0.169, p = < 0.0001) but not in the *remnants* ($\beta$ =0.147, Std. Error = 0.181, p=0.42).

### 4.2 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. 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 Appendix Table 8).

### 4.3 Impact of clearfelling on epiphytic lichens

#### 4.3.1 Short- and mid-term effects on lichen vitality measured by chlorophyll fluorescence yield

In the autumn following conifer removal, significantly lower (by c.40%) chlorophyll fluorescence (CF) yield was observed for both *L pulmonaria* and *L virens* 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).

#### 4.3.2 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 (Appendix Table 9).

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).

## 5 Discussion

### 5.1 Overview

In the nine years following restoration management, revegetation 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.

### 5.2 Ground vegetation response measures of restoration success and timeframe of restoration

#### 5.2.1 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 Naaf 2015; Naaf 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 (*Picea abies*)-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.

#### 5.2.2 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 et al. 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 et al. 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).

#### 5.2.3 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 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.

### 5.3 Lichen response

#### 5.3.1 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).

#### 5.3.2 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 centre 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. 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 recolonization 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.

## 6 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 59,000 ha 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), to which our study results are most applicable. 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).

# Appendix

## Methods

### Climatic data for Scottish oak woodlands

Mean monthly temperature and rainfall data for Glencripesdale (data for the period 2007 to 2016 from the nearest meteorological weather station (Dunstaffnage): 56° 45' N, 5° 44' W) is shown in Fig. 5. Mean monthly temperature rarely exceeds 15 °C or falls below 5 °C and rainfall exceeds 100 mm during nine months of the year, exceeding 200 mm in three of these. Glencripesdale occurs within the area of the British Isles where the *Western Scotland Index of Ecological Continuity* for ancient deciduous woodlands applies (Coppins and Coppins 2002); the *Eastern Scotland*

*Index of Ecological Continuity* and the *New Index of Ecological Continuity* applies to oak woodlands in other parts of Scotland (Table 3).

Three climatic indices[1] were calculated for 10 oak woodland sites, including Glencripesdale, in order to inform how we can extrapolate the results of our study site in terms of the likely effects on growing conditions created by sudden opening up of the tree canopy, to other oak woodlands experiencing a similar intervention. At Glencripesdale, the mean continentality is comparable to all the other woodlands considered. Climatic warmth, the amount of yearly growing degrees (for all days of mean temperature above 5 °C, the sum of the degrees above 5 °C) at Glencripesdale was similar to most oak woodland sites with only two sites being significantly cooler (Comrie and Mudock). However, when mean annual heat:moisture index is considered (high index values where low precipitation relative to temperature; low index values where high precipitation relative to temperature), Glencripesdale was similar to three sites (Loch Maree, Mugdock and Comrie), but index values were lower than for three (Alvie, Dinnet and Wood of Cree) and higher than for two (Benmore and Glen Nant). We consider that between 2007 and 2016, the climate of Glencripesdale, compared to other oak woodland sites in Scotland (data also from the (nearest meteorological weather stations) (Table 3), is at the higher end of the range for climatic warmth but has a median value for heat: moisture index, indicating the effect of high levels of precipitation on maintaining an oceanic climate typical of oakwoods in western Scotland. The range of values for these climate indices is however small and rarely are the values for Glencripesdale significantly different from those of the other oak woodland sites. In this respect, Glencripesdale presented a somewhat median climate and our results could be extrapolated to a number of oak woodland sites.

### Chlorophyll fluorescence measures and calculation

Parameter settings of the pulse amplitude moderated (PAM) chlorophyll fluorimeter in this study used a controlled illumination protocol after dark adaptation of the thalli. The application of basic fluorimetry of dark-adapted samples (Fv/Fm) has been published for *Lobaria pulmonaria (*Palmqvist and Sundberg 2000). In this investigation, we employed more complex assessments of light utilisation by the *Lobarion* lichen species on remnants in PAWS and ASNW trees offering various microsites. After dark-adapting the lichen thalli for 30 min, maximal photochemical utilisation (ΦPSII), after 90 s exposure to 400 μmol $m^{-2}$ $s^{-1}$ of constant illumination, was recorded. Quantum efficiencies of photosystem II photochemistry parameter, measured under illuminated conditions, were calculated following van Kooten and Snel (1990), where $\Phi PSII = Fv'/Fm' * qp$.

### Lichen cover sampling and data analysis

Atlantic oak woodland lichen communities present at the study site were identified in a pre-survey in 2005 (Table 4), for full details see Thompson and Hope 2005. To this list, we have added the lichens that were recorded from the sample patches during our study (2007 to 2016). We assigned a conservatism coefficient to each lichen (see footnotes to Table 4) following the methodology of Reemts and Eidson (2019).

Lichen patch location and extent was delineated by placing a PVC 0.04 $m^2$ frame around each patch. The frame was precisely relocated at each assessment time by means of three plastic nails set into the bark; for smaller lichen patches, a half-frame measuring 0.02 $m^2$ was used. The patches were photographed with a 10-megapixel, hand-held digital field camera. Setting up a tripod was not deemed feasible on the steep slopes and the lighting could not be homogenized, but these adjustments were not considered necessary for the assessment of lichen surface area.

Trimble's ©E-cognition carries out object-based classification as opposed to pixel-based and is mostly used in the analysis of high resolution spatial imagery (Darwish et al. 2003; Liu and Xia 2010; Myint et al. 2011). Each photo was primarily subjected to a personalised multi-resolution segmentation, for which ©E-cognition is renowned, in order to extract the individual elements as objects. These were classified by the software using a rule set which was constructed using various object features related to colour, shape and texture. A kappa-coefficient for agreement and an estimate of classification accuracy were calculated per class per photo by comparing the automatic and manual classification of objects sampled at random. These were extracted along with the total surface area per class. The classification was only accepted if the overall kappa-coefficient exceeded 0.7 and if the class-specific kappa-coefficient exceeded 0.6. Differences in cover were calculated between 2008 and 2016 for each lichen in each frame and expressed as $cm^2$ of lichen cover and as a percentage of frame cover. Absolute differences lower than 3% are recorded but arbitrarily not considered of importance, as variability of the photographed area due to tree growth and segmentation error could not be completely removed.

[1] Biologically relevant climate indices and supporting variables

| | |
|---|---|
| Continentality (°C; difference between MWMT and MCMT) | |
| Annual heat: moisture index (MAT+10)/(MAP/1000) | |
| Degree days above 5(°C) | |
| Mean annual temperature (°C) | MAT |
| Mean warmest month temperature (°C) | MWMT |
| Mean coldest month temperature (°C) | MCMT |
| Mean annual precipitation (mm) | MAP |

http://raster.climatebc.ca/download/List_of_climate_variables.pdf

## Results

### Ground flora indicator species

**Table 6** Proportion (p̂) of quadrats containing each of the indicator species with 95% confidence intervals (C.I.) for *remnant* and *former plantation* sample areas in 2008 and 2016

| | Remnant | | | | Former plantation | | | |
|---|---|---|---|---|---|---|---|---|
| | 2008 | | 2016 | | 2008 | | 2016 | |
| Species | p̂ | 95% CI | p̂ | 95% CI | p̂ | 95% CI | p̂ | 95% CI |
| *Agrostis capillaris* | 0.28 | 0.07–0.48 | 0.28 | 0.07–0.48 | 0.04 | 0–0.09 | 0.17 | 0.07–0.27 |
| *Anthoxanthum odoratum* | 0.06 | 0–0.16 | 0.06 | 0–0.16 | 0.00 | – | 0.07 | 0–0.14 |
| *Blechnum spicant* | 0.00 | – | 0.06 | 0–0.16 | 0.02 | 0–0.05 | 0.07 | 0–0.14 |
| *Calluna vulgaris* | 0.00 | – | 0.06 | 0–0.16 | 0.00 | – | 0.00 | – |
| *Chrysosplenium oppositifolium* | 0.06 | 0–0.16 | 0.06 | 0–0.16 | 0.00 | – | 0.00 | – |
| *Cirsium palustre* | 0.11 | 0–0.26 | 0.00 | – | 0.00 | – | 0.02 | 0–0.05 |
| *Deschampsia cespitosa* | 0.11 | 0–0.26 | 0.22 | 0.03–0.41 | 0.00 | – | 0.48 | 0.35–0.61 |
| *Deschampsia flexuosa* | 0.11 | 0–0.26 | 0.22 | 0.03–0.41 | 0.00 | – | 0.04 | 0–0.09 |
| *Dryopteris dilatata* | 0.06 | 0–0.16 | 0.22 | 0.03–0.41 | 0.00 | – | 0.17 | 0.07–0.27 |
| *Dryopteris filix-mas* | 0.00 | – | 0.00 | – | 0.00 | – | 0.04 | 0–0.09 |
| *Galium saxatile* | 0.11 | 0–0.26 | 0.22 | 0.03–0.41 | 0.00 | – | 0.02 | 0–0.05 |
| *Geranium robertianum* | 0.06 | 0–0.16 | 0.06 | 0–0.16 | 0.00 | – | 0.00 | – |
| *Geum urbanum* | 0.00 | – | 0.06 | 0–0.16 | 0.00 | – | 0.00 | – |
| *Holcus lanatus* | 0.06 | 0–0.16 | 0.44 | 0.21–0.67 | 0.00 | – | 0.54 | 0.4–0.67 |
| *Holcus mollis* | 0.28 | 0.07–0.48 | 0.00 | – | 0.04 | 0–0.09 | 0.04 | 0–0.09 |
| *Hyacinthoides non-scripta* | 0.00 | – | 0.06 | 0–0.16 | 0.00 | – | 0.02 | 0–0.05 |
| *Juncus effusus* | 0.11 | 0–0.26 | 0.11 | 0–0.26 | 0.11 | 0.03–0.19 | 0.26 | 0.14–0.38 |
| *Lysimachia nemorum* | 0.11 | 0–0.26 | 0.11 | 0–0.26 | 0.00 | – | 0.17 | 0.07–0.27 |
| *Oxalis acetosella* | 0.61 | 0.39–0.84 | 0.61 | 0.39–0.84 | 0.41 | 0.28–0.54 | 0.46 | 0.33–0.6 |
| *Poa trivialis* | 0.28 | 0.07–0.48 | 0.28 | 0.07–0.48 | 0.04 | 0–0.09 | 0.04 | 0–0.09 |
| *Potentilla erecta* | 0.00 | – | 0.06 | 0–0.16 | 0.00 | – | 0.11 | 0.03–0.19 |
| *Primula vulgaris* | 0.22 | 0.03–0.41 | 0.06 | 0–0.16 | 0.07 | 0–0.14 | 0.04 | 0–0.09 |
| *Pteridium aquilinum* | 0.06 | 0–0.16 | 0.06 | 0–0.16 | 0.02 | 0–0.05 | 0.24 | 0.13–0.35 |
| *Ranunculus repens* | 0.11 | 0–0.26 | 0.22 | 0.03–0.41 | 0.00 | – | 0.04 | 0–0.09 |
| *Veronica chamaedrys* | 0.06 | 0–0.16 | 0.06 | 0–0.16 | 0.02 | 0–0.05 | 0.00 | – |
| *Viola riviniana* | 0.33 | 0.12–0.55 | 0.11 | 0–0.26 | 0.06 | 0–0.12 | 0.20 | 0.1–0.31 |

### Interpretation of ground flora community composition using species traits

**Table 7** Summary statistics for RLQ analysis (Dray and Dufour 2007)

| RLQ | Eigenvalue | Covariance | Correlation |
|---|---|---|---|
| 1 | 0.62 | 0.79 | 0.53 |
| 2 | 0.07 | 0.26 | 0.22 |

## Lichen assessment

**Table 8** Association between species traits and environment where environment (Site) is combinations of location (*former plantation* or *remnant*) x year (2008 or 2016) and traits are Ellenberg values for light, moisture and nitrogen (Hill 1999) and Grime strategy C-S-R values (Hunt et al. 2004)

| Test | Obs | Std.Obs | Pvalue | Pvalue.adj |
|---|---|---|---|---|
| Site.Former Plantation 2008 / Light | − 0.352 | − 1.792 | 0.065 | 0.296 |
| Site.Former Plantation 2016 / Light | 0.220 | 1.300 | 0.202 | 0.539 |
| Site.Remnant 2008 / Light | − 0.053 | − 0.497 | 0.638 | 0.766 |
| Site.Remnant 2016 / Light | 0.079 | 0.921 | 0.364 | 0.667 |
| Site.Former Plantation 2008 / Moisture | − 0.103 | − 0.532 | 0.632 | 0.766 |
| Site.Former Plantation 2016 / Moisture | 0.084 | 0.521 | 0.628 | 0.766 |
| Site.Remnant 2008 / Moisture | − 0.051 | − 0.513 | 0.619 | 0.766 |
| Site.Remnant 2016 / Moisture | 0.027 | 0.280 | 0.792 | 0.875 |
| Site.Former Plantation 2008 / Nitrogen | 0.011 | 0.055 | 0.958 | 0.975 |
| Site.Former Plantation 2016 / Nitrogen | − 0.006 | − 0.034 | 0.975 | 0.975 |
| Site.Remnant 2008 / Nitrogen | − 0.089 | − 0.871 | 0.394 | 0.667 |
| Site.Remnant 2016 / Nitrogen | 0.073 | 0.836 | 0.417 | 0.667 |
| Site.Former Plantation 2008 / C | − 0.424 | − 2.172 | 0.024 | 0.157 |
| Site.Former Plantation 2016 / C | 0.427 | 2.556 | 0.004 | 0.047 |
| Site.Remnant 2008 / C | − 0.103 | − 1.007 | 0.324 | 0.667 |
| Site.Remnant 2016 / C | − 0.093 | − 1.092 | 0.283 | 0.667 |
| Site.Former Plantation 2008 / S | 0.303 | 1.540 | 0.131 | 0.448 |
| Site.Former Plantation 2016 / S | − 0.163 | − 0.962 | 0.352 | 0.667 |
| Site.Remnant 2008 / S | − 0.026 | − 0.265 | 0.802 | 0.875 |
| Site.Remnant 2016 / S | − 0.044 | − 0.514 | 0.618 | 0.766 |
| Site.Former Plantation 2008 / R | 0.282 | 1.425 | 0.166 | 0.499 |
| Site.Former Plantation 2016 / R | − 0.448 | − 2.652 | 0.004 | 0.047 |
| Site.Remnant 2008 / R | 0.183 | 1.774 | 0.074 | 0.296 |
| Site.Remnant 2016 / R | 0.189 | 2.180 | 0.026 | 0.157 |

**Table 9** Lichen community diversity metrics of average conservatism and species richness and tests for differences between metrics assessed for *ASNW* (n = 8) and *remnants* (n = 14) and between the two years of assessment in 2007 and 2016.

| | | Average conservatism | | | | Species richness | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean ± SE (in 2007 & 2016) | | Test of difference between ASNW and Remnants (Mann-Whitney) | | Mean ±SE (in 2007 & 2016) | | Test of difference between ASNW and Remnants (Mann-Whitney) | |
| | | ASNW | Remnants | U statistic | P value | ASNW | Remnants | U statistic | P value |
| Year | 2007 | 3.205 ± 0.2818 | 4.129 ± 0.3143 | 27.00 | p = 0.0331 | 2.375 ± 0.3239 | 2.0 ± 0.2774 | 43.50 | p = 0.3824 |
| | 2016 | 3.29 ± 0.3240 | 4.19 ± 0.4875 | 30.00 | p = 0.0353 | 1.75 ± 0.3134 | 1.5 ± 0.2285 | 48.00 | p = 0.5788 |
| Test of change over time - 2007 to 2016 (Mann-Whitney) | U statistic | 30.00 | 98.00 | | | 20.00 | 73.00 | | |
| | P value | p = 0.8678 | p = 0.9770 | | | p = 0.1929 | p = 0.2290 | | |

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**Data availability** The datasets generated during and/or analysed during the current study are not publicly available due to data being used in a follow-up manuscript but are available from the corresponding author on reasonable request.

## Declarations

**Ethics approval** The authors declare that they obtained the approval of Nature Scot's Protected Areas Committee for conducting the study in 'Glencripesdale National Nature Reserve'.

**Conflict of interest** The authors declare no competing interests.

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