

The diversity and community dynamics of hazelwood lichens and bryophytes along a major gradient of human impact

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Background: Oceanic hazelwoods in western Scotland are hypothesised to be unmanaged post-glacial relicts, representing an unusual type of old-growth forest habitat in Europe. They are characterised by an exceptionally high epiphytic diversity, including their status as ‘hotspots’ for indicators of woodland ecological continuity.

Aims: The aim of this study was to evaluate the effects of climate, pollution and management on the occurrence of epiphytic lichens and bryophytes on *Corylus avellana*.

Methods: Thirteen hazelwood study sites were systematically sampled along a climate, pollution and management gradient in Britain. Epiphyte composition and richness were examined in a strict hierarchical framework, and compared against site-, stool- and stem-scale environmental predictors.

Results: The study showed that along the gradient from ‘clean-air’ relict sites to ‘polluted’ coppiced sites: (i) epiphytic local stem-scale diversity declined, (ii) there was a loss of late-successional species including foliose cyano- and tripartite lichens and bryophytes and (iii) stem sizes were reduced, providing a further limit to the accumulation of species richness within a site.

Conclusions: Relict hazelwoods in western Scotland are confirmed as an example of the most intact epiphyte communities. In particular, we show that the transition to coppicing can be clearly linked to ecological processes causing species loss.

Keywords: bryophytes; climate gradient; ecological continuity; epiphytes; lichens; forest management; SO₂ pollution; species richness; succession

Introduction

Anthropogenic disturbance is the greatest widespread threat to biodiversity (Hannah et al. 1995; MEA 2005). In temperate Europe, this threat emerges from a long-term process of extensive deforestation initiated by Neolithic cultures (Birks 1988; Williams 2000), as well as the more recent impact of transboundary air pollution and a shift towards intensification of landscape management during the Industrial Revolution (Crutzen 2002; Steffen et al. 2007).

In the context of forest loss, traditionally managed European ancient woodlands have become a priority conservation resource. Examples, such as ancient parkland or pasture woodland (Rackham 2003), have existed over long time periods and retain structural properties that are thought to be similar to ‘natural’ old-growth stands, such as overmature and senescent trees in gladed settings. Where they continue to exist in the landscape, these ancient woodland characteristics have allowed the survival of niche specialists (Peterken 1974; Hermy et al. 1999), among the most important of which are lichen and bryophyte epiphytes (Rose 1976, 1993). These epiphytic organisms are diverse in forest and woodland habitats and their occurrence is controlled by environmental conditions both at the tree scale related to the quality of the host tree on which they grow (e.g. tree diameter, bark

roughness, bark pH), and at the stand scale related to tree species composition and density for stands in which they occur (Ellis 2012). However, the presence of certain species with a dependency on old-growth structure and/or temporal continuity of woodland sites (Josefsson et al. 2005) provides a signature for high conservation status habitat (Ferris and Humphrey 1999; Gustafsson et al. 1999).

In the context of industrial change, woodland indicators including lichen and bryophyte epiphytes are known to be sensitive to the pollution regime (Hawksworth and Rose 1970; Van Herk et al. 2003). Industrialisation has caused the loss of ‘old-growth’ epiphytic diversity in regions where suitable woodland structure exists, but levels of air pollution are damaging (Ellis et al. 2014). Furthermore, lichen and bryophyte indicators occurring on older trees, and/or in stands with temporal continuity, are sensitive to both (i) rotational forestry, such as coppicing, which has turned natural forests into structurally simplified even-aged stands (Nascimbene et al. 2009, 2013) as well as (ii) the abandonment of traditional management, which can result in shading via secondary succession and the loss of epiphytes that are associated with open canopy structures (Leppik et al. 2011; Paltto et al. 2011).

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Observational studies that draw on the diversity of lichen epiphytes to infer structural stability and levels of temporal continuity (Coppins and Coppins 2002), have suggested that a small number of remote hazelwoods (*Corylus avellana* L.) on the west coast of Scotland are likely to have existed as practically undisturbed self-sustaining ecosystems throughout the post-glacial period (Coppins and Coppins 2003, 2012). Hazel is native to and occurs throughout Britain, being naturally absent only from higher montane systems and peatlands (Preston et al. 2002). It is a light-demanding multi-stemmed shrub, with more than one stem arising from each individual rootstock or stool. Hazel has been intensively managed since at least early Mediaeval times, especially in lowland England (Rackham 2003); coppicing of hazel was regularly carried out, typically on a 7-year cycle, with young hazel stems producing an 'underwood' product. However, this intensive management of hazel, as part of a community woodland resource, contrasts with the concept of hazelwoods as the natural 'climax' community in western Scotland, western Ireland and rarely in south-west England and Wales (Gilbert 1984; Coppins and Coppins 2003, 2012), and which persist through an autogenic process of self-coppicing. The proposition that hazelwoods in the west coast of Scotland are post-glacial relict positions these ecosystems at one end of a broad spectrum of environmental gradients that encompass: (i) old-growth to intensively managed systems, (ii) oceanic temperate rainforest to lowland drier and more continental sites in midland and southern England and (iii) relatively clean-air localities through to sites with higher levels of air pollution. Thus, hazel occurs widely along a gradient that is representative of major human impacts, as discussed above, and so provides a useful system for studies in epiphyte ecology.

This study documents for the first time the gradient of human impact as it relates to hazelwoods in Britain, and in doing so, it compares the epiphyte community structure of putative old-growth hazelwoods with the more familiar coppiced hazelwoods of lowland England. Many previous epiphyte studies have emphasised human effects at single scales, e.g. exploring trends in composition and richness for sites along regional climate and pollution gradients (McCune et al. 1997; Ellis and Coppins 2009), or related to habitat dynamics within regions or sites (Juriado et al. 2009). In contrast, the distribution of sampled hazelwood sites made it possible to reconstruct processes which affect epiphyte diversity through the interaction of composition and richness over different scales, while integrating the effects of pollution with local management. To place these processes within a hypothesis-driven framework, the study asked the following questions: (i) at a stem-scale, how do values of species richness vary along the gradient of human impact and how might differences in species composition be explained; (ii) at a site-scale, how does richness for stems combine with compositional differences among stems and stools to generate species diversity at a site? What are the major factors explaining differences in

this accumulated diversity when considered along the gradient from 'clean air relict' to polluted and intensively managed sites?

Materials and methods

Study sites and environmental factors

A database of 115 widely distributed hazelwoods in mainland Britain was compiled from literature and internet searches. In all sites, hazel stools dominated either the canopy or occurred as an understorey layer, for an area of ≥ 0.5 ha, and with a minimum of 40 individually identified stools. These sites were matched to 5 km-gridded geographic information system layers for four least correlated variables preselected among a range of potential factors. Climatic and pollution data were summarised using principal component analysis to select variables that were weakly correlated and these described contrasting aspect of the climate and pollution regimes (see Ellis et al. 2014): (i) mean annual temperature and (ii) annual precipitation, both for a baseline period of 1961–2006 made available by the Met Office of the UK (Perry and Hollis 2005) and (iii) atmospheric concentrations of SO₂ as based on a spatial interpolation for both 1987 and 2004–2006 averaged values and (iv) NH_x deposition, using interpolation of 2004–2006 averaged values, made available by the Centre for Ecology and Hydrology, UK (cf. RoTAP 2012). Management varied from putative relict old-growth stands in western Scotland, through sites where hazel is a scattered component of a semi-natural understorey to more intensively managed coppiced sites.

Sampling design and data collection

A total of 13 hazelwood study sites were sampled; two putative clean-air relict sites and 11 other hazelwood sites along a climatic, pollution and management gradient in Britain (Figure 1, Appendix S1). We sampled a total of 788 stems across 191 stools (Appendix S2) during fieldwork in 2012. Epiphytic assemblages were surveyed within both edge and interior habitats, using a hierarchical structure of stems nested within stools, and stools nested within sites. For each site, stools were randomly selected for survey by positioning along random aspects, from a starting point located centrally within each hazel-dominated stand, and ensuring sampled stools were ≥ 10 m apart. On each selected stool, stems were sampled within each of nine size classes: 0–2 cm; 2–4 cm; 4–6 cm; 6–8 cm; 8–10 cm; 10–12 cm; 12–14 cm; 14–16 cm; >16 cm dbh. Stem size for hazel, scales linearly with ring count as a proxy for age (Eaton and Ellis 2014). For an individual stool, a random start point was selected between 0° and 360°, with sampling progressing clockwise to accumulate consecutive stems along the direction of travel and aiming to sample for each stool a single stem in each size class. Up to 10 stems per size class were sampled per site across a maximum of 60 hazel stools.

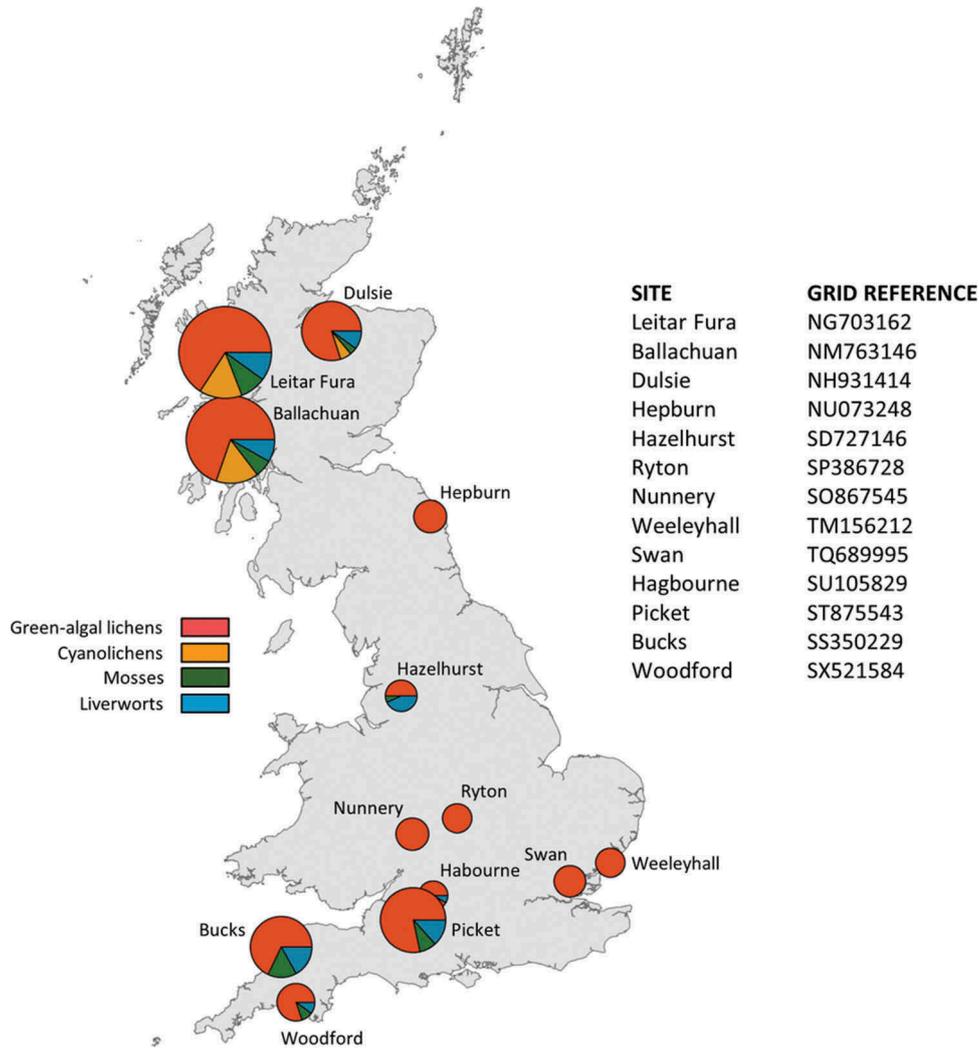


Figure 1. Distribution of the 13 hazel stands studied in mainland Britain including the relative proportion of species richness.

On each of the sampled stems, the frequency of epiphytic lichens and bryophytes was estimated using a ladder transect of 1 cm × 5 cm squares, placed at 1.3 m height on four different aspects (N, S, E, W). Additional ladders were sampled at randomly selected intermediate aspects for progressively larger stems to ensure that the sampling effort was related to the available habitat area.

Statistical analyses

Generalised linear mixed models (GLMM) were used to compare the epiphyte community richness of a hazel stem to seven environmental predictors operating at each hierarchical spatial scale (site, stool and stem; stems nested within stools and stools nested within sites). The selected environmental predictors were: SO₂, NH_x, mean temperature and annual precipitation at the site level, canopy openness and stand type coded as edge/interior at the stool level, and dbh at the stem level. We derived eight different estimates of species richness and carried out separate analyses of each estimate: (i) total species richness, (ii) epiphytic lichens, (iii) epiphytic bryophytes, (iv) cyano- and tripartite lichens, (v) mosses, (vi)

liverworts, (vii) indicators of woodland ecological continuity (Coppins and Coppins 2002) and (viii) pollution sensitive indicators (Smith et al. 2009; Atherton et al. 2010). Environmental predictors were included as explanatory variables (fixed effects), and ‘site’ and ‘stool’ were treated as random sources of variation as appropriate. We fitted GLMM with a Poisson error distribution and a log-link function. Backward elimination from a full model, with log-likelihood tests, was used to select the final model for species richness (Zuur et al. 2009); all variables with $P < 0.05$ were retained in the final model. Akaike’s information criterion (AIC) (Akaike 1973) and the significance of the fixed effects were therefore used to identify an optimal parameterisation of the models (Shao 1997). We used the free software R (v 3.0.1; R Development CoreTeam 2013) for the statistical analyses with library ‘lme4’ (Bates et al. 2008).

We used sample-based rarefaction curves, scaled by the number of stems, to compare epiphyte species richness among the 13 studied hazelwoods and controlling for the different number of stems surveyed (Gotelli and Colwell 2001). Statistical comparison of species richness for a comparable level of sampling effort was tested by comparing confidence

limits for the curves; differences are not significant at $P < 0.05$ if the confidence intervals overlap (Gotelli and Colwell 2001). The curves were produced using EstimateS version 9.10 (Colwell 2013) and calculated with resampling 100 times.

Canonical correspondence analysis (CCA) was carried out to test the null hypothesis that epiphyte composition was independent of the environmental predictors (DCA, 7.6 standard deviation units; Legendre and Anderson 1999). All analyses were implemented using CANOCO v. 4.5 (Ter Braak and Šmilauer 1997). Analyses were run using a reduced species matrix that excluded rare species (species occurring on <5 stems). Environmental predictors were grouped at their respective scale: site, stool and stem. A total of three CCAs were conducted, one to reflect each environmental scale and with down weighting of rare species. The sum of all canonical eigenvalues (or trace) was used to build the F -ratio statistic (Legendre and Anderson 1999), which was then used to estimate the overall level of significance with a Monte Carlo test of 999 randomisations. A forward stepwise procedure was subsequently used to select significant predictors. Variables were selected sequentially in order of decreasing eigenvalue, until any new variable was non-significant ($P > 0.05$). Improvement of the reduced model with each new selected variable was determined by a Monte Carlo test (999 randomisations). Partial CCA (Ter Braak and Šmilauer 1997) was conducted to evaluate the relative importance of each of the sets of environmental predictors after adjusting for the effect of the covariable sets (Legendre and Legendre 1998).

In order to explain community contrasts relating stem diameter to epiphyte functional traits, we used multivariate plots for CCA at contrasting scales including overlays for the weighted mean trait composition of the samples. We considered three bryophyte growth forms: acrocarpous mosses (ACRO), pleurocarpous mosses (PLEURO) and liverworts (LIVER). Lichen epiphytes were classified into nine functional groups based on the growth form, reproductive strategy (reproductive mode and associated diaspore size) and photosynthetic partner: non-lichenised ascomycete fungi (NON), crustose lichens with perithecia (PERI), crustose lichens with lirellae (LIRE), crustose lichens with apothecia (APO), asexual crustose lichens (ASEX), fruticose lichens

(FRUTI), leprose lichens (LEPRO), green-algal foliose (FOLIO) and foliose cyano- and tripartite lichens (CYANO). Trait characteristics were coded for each species based on descriptions in the British lichen and bryophyte floras (Smith et al. 2009; Atherton et al. 2010).

Finally, a Mantel test was employed to test for goodness of fit in each sampled site between two pairwise matrices, a Jaccard dissimilarity matrix for community composition and an environmental matrix which computed the diameter difference between two stems. Here, the idea was to determine whether epiphyte communities for similar stem diameters showed greater similarity than communities in stems that were more different in their size. We used the R environment (v. 3.0.1; R Development Core Team 2013) for statistical analyses. The species dissimilarity matrices were obtained with the “*vegdis*” function of the “*vegan*” package (Oksanen et al. 2013). Mantel tests were calculated using the “*mantel*” function implemented in the “*vegan*” package (Oksanen et al. 2013), and significance was assessed using a permutation test with 999 randomisations.

Results

The sampling recorded 165 epiphytes; this included 139 lichen species, the majority of which were sexually reproducing crustose growth forms (Figure 2(a)). Foliose lichens were the second most common growth form, including 27 cyano- and tripartite lichens. In terms of the conservation status of lichen samples (Woods and Coppins 2012), the data set included five Biodiversity Action Plan Species, 28 species for which the UK has an international responsibility towards their conservation and one IUCN categorised vulnerable species (Appendix S2). There were 27 lichen indicators of woodland ecological continuity (Coppins and Coppins 2002), and 16 pollution indicators (Smith et al. 2009; Atherton et al. 2010), as well as 19 species that appear to grow mainly on *Corylus avellana* in Europe (Appendix S2). The sampling recorded 26 bryophytes (Figure 2(b)), equally split among the mosses and liverworts. We found five species that are indicators of an oceanic flora and rare or absent in the east. The most common epiphytes (occurring on $\geq 12\%$ of sampled

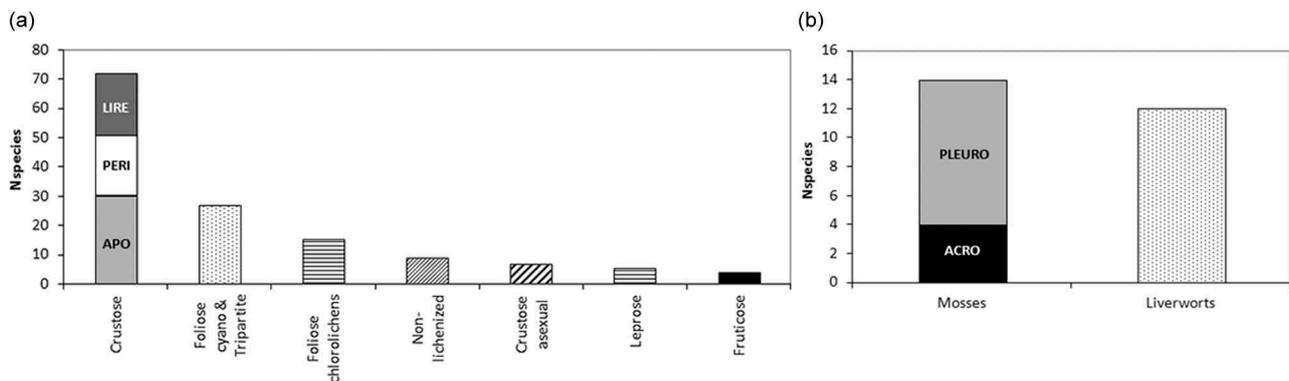


Figure 2. Epiphytic functional group composition sampled from hazelwoods: (a) lichens; (b) bryophytes.

stems) were: *Arthonia didyma*, *A. spadicea*, *Leptorhaphis maggiana*, *Lepraria incana*, *Pertusaria leioplaca*, *Metzgeria furcata* and *Frullania dilatata*.

Species richness

In terms of variability in the epiphyte community richness recorded for individual hazel stems, sulphur dioxide (SO₂) and annual precipitation were the significant site-scale environmental predictors. Sulphur dioxide was negatively correlated to the total diversity and the sub-divided categories of lichen richness, cyano- and tripartite lichen richness, and as expected the richness of pollution sensitive species. Annual precipitation positively influenced the richness of bryophytes, including the subcategories for mosses and liverworts separately, and the richness of woodland ecological continuity indicators (Table 1). Examined for the stool-scale predictors (with site as a random effect), decreasing canopy cover had a positive effect on total richness and lichen richness, and a negative effect on the richness of cyano- and tripartite lichens and indicators of woodland ecological continuity, while the richness of pollution sensitive species was lower for interior than for edge environments. At the stem-scale (with site and stool identity as random effects), the richness of all the sub-categories except woodland ecological continuity indicators was positively related to stem size (Table 1; Figure 3).

Putative old-growth hazelwoods on the west coast of Scotland (Ballachuan and Leitar Fura) had the highest observed and estimated richness values corrected for sampling effort (Figure 4), and it is notable that cyano- and tripartite lichens were found mainly in the western Scottish sites (Figure 1, Appendix S2). There were two southern and relatively more polluted sites that had a representation of stems in most size classes, though with proportionally fewer stems of the largest sizes compared with the very richest sites, while the Dulsie site lacked the largest sized stems but had a cleaner-air environment (Figure 1). The remaining more intensively coppiced sites all had the lowest richness values consistent with species-poor epiphyte

communities, and bryophytes were almost absent (Figure 1, Appendix S2).

Community composition

All three CCA models evaluated were significant ($P < 0.05$), suggesting that environmental variables considered at different spatial scales (i.e. site, stool and stem; Table 2) explained differences in epiphyte species composition. As expected for our large sample size, the total variation explained was rather low: 6.7% for the site-scale variables, 1.1% for the stand-scale data set and 1.8% for the stem-scale variables.

At a site-scale, annual precipitation was the most important variable explaining species composition followed by pollution variables and mean temperature (Table 2; Figure 5(a)). For example, cyanolichens (e.g. *Collema subflaccidum*, *Degelia atlantica* and *Pannaria conoplea*) and oceanic bryophytes (e.g. *Drepanolejeunea hamatifolia*, *Neckera pumila* and *Ulota phyllantha*) were correlated with high rainfall values and low pollution levels. A further group of crustose lichens was sensitive to pollution, but was more abundant in environments with lower humidity, including *Arthopyrenia cerasi*, *A. punctiformis*, *Arthonia radiata* and *Pertusaria amara*. A pollution-tolerant group of species included *Candelariella reflexa*, *Physcia tenella*, *Porina aenea* and *Xanthoria parietina*, all of which are characterised by their ability to colonise a wide range of nutrient-enriched microhabitats.

At a stool-scale, canopy openness was the most important variable followed by the edge or interior woodland environment (Table 2, Figure 5(b)), with a difference between species that appeared shade tolerant (*Isothecium myosuroides*, *Lobaria virens*, *Megalania pulvereana* and *Neckera complanata*) and those which appeared relatively light demanding (*Hypnum cupressiforme*, *Isothecium alopecuroides*, *Pertusaria multipuncta* and *Sticta fuliginosa*).

At a stem-scale, stem size was important in explaining differences in species composition (Table 2). The grouping

Table 1. Results for generalised linear mixed models (GLMMs) used to explain species richness of hazel stems. Predictors were included as explanatory variables (fixed factors), and site- and stool-identity were treated as random sources of variation.

Variable	Total	Lichen	Bryophyte	Cyano- and tripartite lichen	Moss	Liverwort	Old-woodland	Pollution sensitive
(a) Site level								
SO ₂	-3.459***	-3.137**	ns	-1.850 ~	ns	ns	ns	-2.630**
NH _x	ns	ns	ns	ns	ns	ns	ns	ns
Tmean	ns	ns	ns	ns	ns	ns	ns	ns
Pann	ns	ns	3.662***	ns	3.521***	3.488***	3.868***	ns
(b) Stool level								
Canopy	3.116 **	3.914 ***	ns	-2.307 *	ns	ns	-2.167*	ns
INT	ns	ns	ns	ns	ns	ns	ns	-3.381***
(c) Stem level								
DBH	12.606 ***	7.049 ***	11.246 ***	6.655 ***	10.383 ***	8.407 ***	ns	7.036 ***
Intercept	4.739 ***	4.627 ***	-5.247 ***	ns	-5.502 ***	-5.431 ***	-5.551 ***	ns

Pann: annual precipitation (mm); SO₂: sulphur dioxide levels ($\mu\text{g kg}^{-1}$); NH_x: nitrogen levels ($\text{kgN}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$); Tmean: mean temperature (°C); Canopy: canopy openness; INT: interior environment, DBH: stem diameter (cm). The table shows the sign and value of fixed effects, and their significance for the optimised models: ***: $P < 0.0001$, **: $P < 0.001$, *: $P < 0.01$, ~: $P < 0.05$, ns: non-significant.

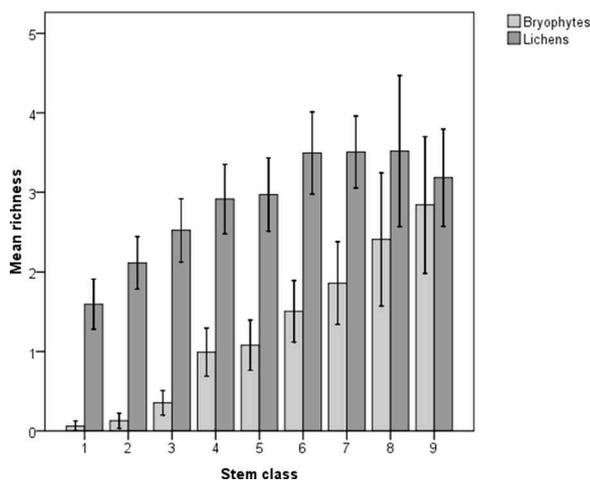


Figure 3. The relationship between lichen and bryophyte richness (cf. Table 1), plotted as a summary for pooled site data. Correlation coefficients for Spearman rank tests: lichens ($r = 0.269$, $N = 681$, $P = < 0.01$); bryophytes ($r = 0.487$, $N = 249$, $P = < 0.01$). Stem diameter classes: (1) 0–2 cm; (2) 2–4 cm; (3) 4–6 cm; (4) 6–8 cm; (5) 8–10 cm; (6) 10–12 cm; (7) 12–14 cm; (8) 14–16 cm; (9) >16 cm.

of species by their functional characteristics revealed a clear successional gradient from young (small) to old (large) stems (Figure 5(c)), evidenced by the transition: non-lichenised ascomycetes, crustose lichens with perithecia, crustose lichens with lirellae, fruticose lichens, crustose lichens with apothecia, pleurocarpous mosses, liverworts, cyano- and tripartite lichens, green-algal foliose lichens, acrocarpous mosses, leprose lichens and asexual crustose lichens. Finally, the Mantel correlation test for epiphytic composition and the stem diameter differences were significant for all sites (ranging from a correlation of 0.143–0.328, with $P = < 0.002$). Stems more similar in diameter had similar epiphyte species composition.

Discussion

Our study provides empirical support for the conservation value of hazelwood sites in oceanic western Scotland with the highest levels of epiphytic diversity, including species with extremely restricted distributions and/or which are indicators of woodland ecological continuity (Gilbert 1984; Coppins and Coppins 2003, 2012). Since hazel is widely occurring, but has received little attention from epiphyte ecologists previously (though see Grillo and Cristaudo 1995; Ihlen et al. 2001), this study increases our knowledge of epiphytic diversity in Western Europe. The marked differences in species richness depending on the climate, pollution and management support the proposal that there are a substantial number of species highly dependent on well-preserved hazelwoods that become threatened as coppicing or pollution increase. In terms of the overall site-scale species richness, there were three well-defined groups of hazelwoods. First, old-growth

hazelwoods on the west coast of Scotland with the highest observed and estimated richness values. These sites had an oceanic climate, low levels of pollution, and were represented by a full range of stem size classes. Second, semi-natural sites in which hazel formed a dominant though non-intensively managed component of the understory with proportionally fewer stems of the largest sizes compared with the richest sites. Third, intensively coppiced sites in drier and more polluted environments, characterised by species-poor epiphyte communities.

Baseline community structure

Our estimates of richness for hazelwoods in oceanic western Scotland approached c. 100 species even for our limited sub-sampling regime using small-scale quadrats. This value is nearly twice as high as the next richest sites and up to 10 times higher than coppiced sites in polluted environments of lowland England. Species richness and composition for the suite of 13 sampled sites showed statistically significant trends explained by ecological gradients. The oceanic hazelwoods occupied a position at one end of these gradients, and were characterised by comparatively high levels of species richness per stem (alpha-diversity), explained in response to low pollution loads. This stem-scale alpha-diversity acted in combination with a broad successional gradient observed among stems, and leading to the accumulation of different types of species (beta-diversity) across young to old stems. Species composition for oceanic hazelwoods, therefore, included the representation of different trait groups (from sexually reproducing crustose lichens to foliose cyano- and tripartite lichens and bryophytes) across a wider range of stem size classes than was observed at other sites. Analysis showed that the spread of different trait groups across stems of different size/age was sensitive to pollution and management (coppicing), and the absence of these factors for oceanic hazelwoods explained the high species totals (gamma-diversity) observed for the sites at Ballachuan and Leitar Fura (low pollution, no coppicing).

Succession was evidenced by the transition, e.g. in terms of a competition–colonisation trade-off (Cadotte et al. 2006), from pioneer species including sexually-reproducing crustose lichens on smaller stems, through to dominant foliose lichens and bryophytes, which increase in abundance on larger stems. This sorting of species implies that young stems are compositionally more similar to each other than old stems and vice versa. This is consistent with previously described successional trends in epiphyte communities (Boudreault et al. 2000; Sillett et al. 2000) as well as formal tests of epiphyte community assembly (Ellis and Ellis 2013), and matches with the traditional ecological placement of the *Graphidion* and *Lobarion* systems in oceanic woodlands (James et al. 1977). The *Graphidion* refers to smooth bark communities characterised by the dominance of crustose lichen species often with lirellate or pyrenocarpous ascomycetes, and including *Graphina anguina*, *Graphis scripta*,

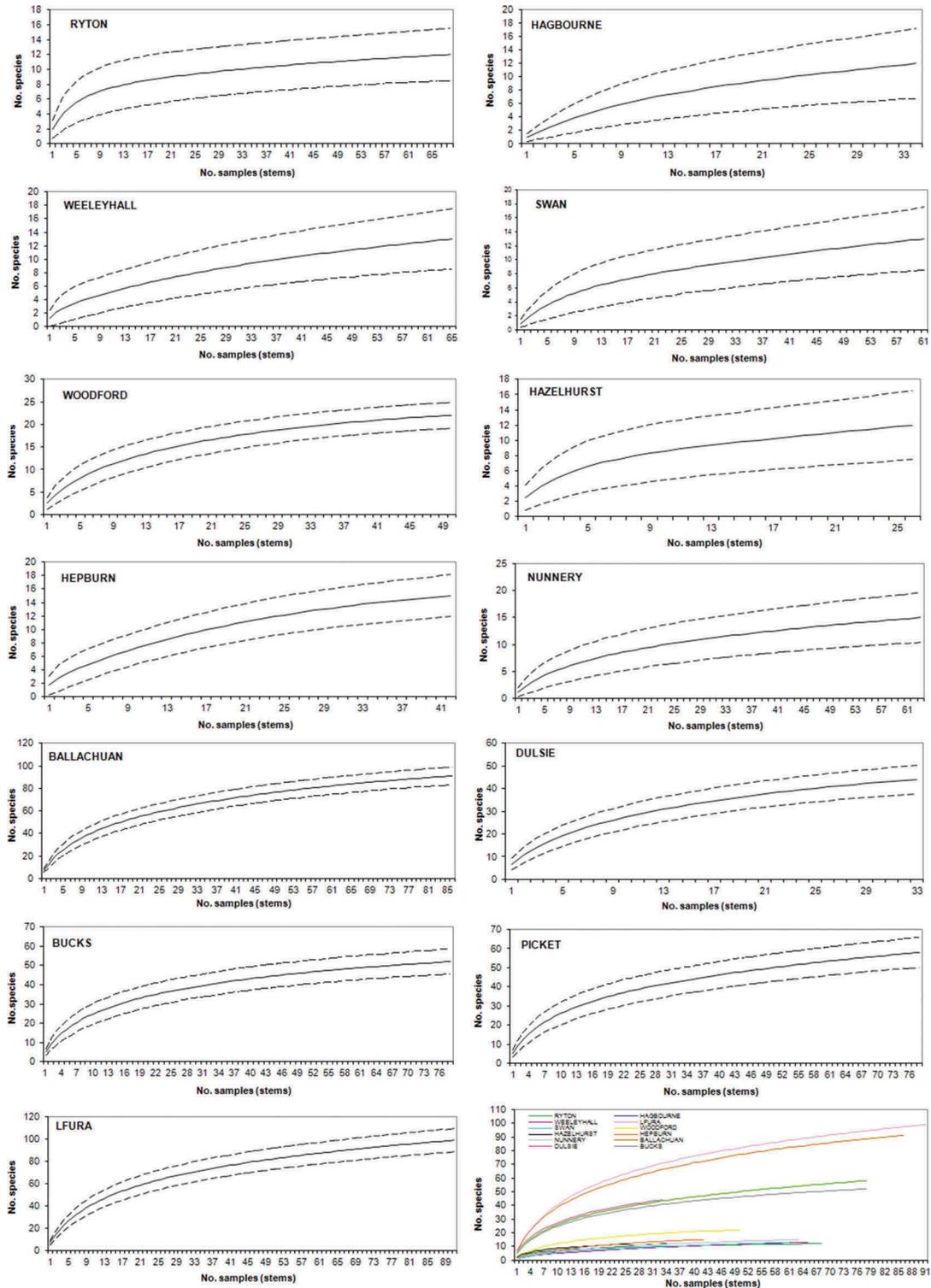


Figure 4. Sample-based accumulation curves comparing species richness per site. The curves show the cumulative number of species with increasing sampling effort. The curves were produced by EstimateS version 9.1 (Colwell 2013) and calculated with 100 random resamples among units (stems).

Pertusaria leioplaca, *P. pertusa*, *Pyrenula nitida*, *P. occidentalis* and *Thelotrema lepadinum*, (James et al. 1977). As stems (or trees) become older, sexual crustose lichens give way to the *Lobarion* community composed mainly of large foliose cyano- and tripartite lichens and bryophytes, which

has been hypothesised to form the natural forest climax on mature trees and is considered the most hygrophytic community (James et al. 1977). We also found evidence for later successional stages dominated by leprose and asexual crustose lichens.

Table 2. Summary of the forward stepwise selection in canonical correspondence analysis (CCA), used to find reduced models including only significant variables.

λ_1	λ_2	λ_3	Σ cons	ICA	TVE	Monte Carlo test	
						<i>F</i> -ratio	<i>P</i>
0.781	0.504	0.424	2.796	1.617	9.69	1.706	0.0010
Variables			Level	λ	<i>F</i> -ratio	<i>P</i>	
Step 1	Pannual	Site	0.59	21.14	0.001		
Step 2	Tmean	Site	0.34	12.35	0.001		
Step 3	DBH	Stem	0.30	12.03	0.001		
Step 4	SO ₂	Site	0.20	7.21	0.001		
Step 5	NH _x	Site	0.17	6.19	0.001		
Step 6	Canopy	Stool	0.12	4.93	0.001		
Step 7	Environment	Stool	0.06	2.31	0.001		

Environ: dummy variable edge/interior. λ_1 , λ_2 and λ_3 : eigenvalues of the corresponding extracted axes; Σ cons: sum of all constrained axes; ICA: sum of all eigenvalues; TVA: total variance explained (in %); *F*-ratio: statistic computed using the trace or sum of all eigenvalues; *P*: level of significance of the method according to Holm’s method ($P < 0.05$). Pann: annual precipitation; Tmean: mean temperature; DBH: stem diameter; SO₂: sulphur dioxide levels; NH_x: nitrogen levels; Canopy: canopy openness; Environment: edge/interior environment.

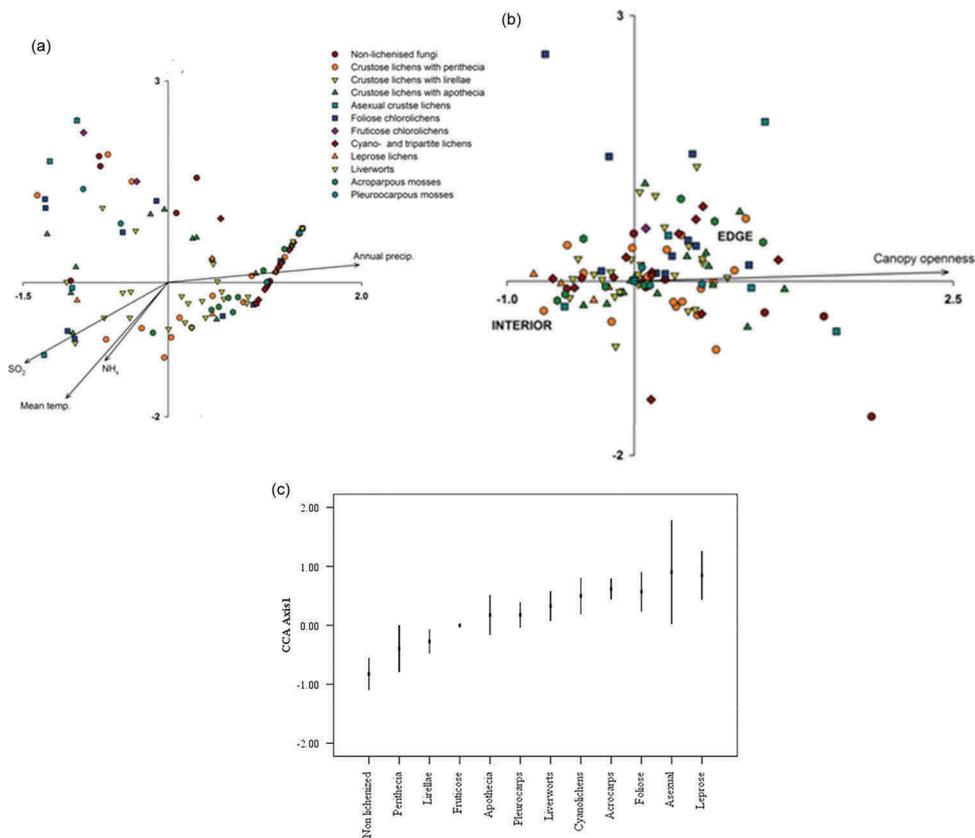


Figure 5. Species–environment biplots for CCA axes 1 and 2. (a) Site-scale variables; (b) stool scale variables and (c) functional group position on the CCA axis 1 for stem diameter (CCA axis 1 mean values are shown with error bars). The vertical bars are interpreted as niche breadths. Only variables selected by the forward stepwise procedure were included. Dummy variables were represented by their centroids.

In addition to the successional system, larger stems also tended to have higher absolute values of species richness (alpha-diversity). This is again consistent with previous results to show that tree size is an important determinant of epiphytic diversity, with larger and older trees maintaining more species per stem than younger trees (Fritz et al.

2008; Nascimbene et al. 2009, 2013). This phenomenon has a potentially complex explanation, however, because larger trees provide a greater colonisation surface (area effect) as well as a longer time period for the establishment and growth of local populations, and increased microhabitat diversity (Fritz et al. 2008; Ranius et al. 2008).

The mechanisms of species loss

Our results highlight that epiphyte community structure is explained by variables across scales, from regional through to microhabitat processes (Fritz et al. 2008; Belinchón et al. 2009), and include a combination of natural variation and human impact. For example, natural variability in climate (annual precipitation) was a site-scale factor that explained the decreasing richness of bryophytes at drier (and tending towards polluted) sites. Bryophyte landscape-scale distribution may be primarily influenced by macroclimatic factors, including rainfall because water availability creates a strong physiological constraint on poikilohydric organisms (Porley and Hodgetts 2005). The same suggestion has been proposed for old-woodland indicators at regional scales (Aragón et al. 2012; Ódor et al. 2013).

Pollution explained the decreasing richness of lichens at sites with higher sulphur dioxide (and which tended to be drier), while noting that sulphur dioxide was operating here as a proxy for a compound gradient that encompassed several covarying pollutants. Atmospheric pollution is established as one of the main factors leading to a decline of epiphytic diversity in Europe (van Dobben et al. 2001). Combining these factors along an impact gradient, the driest and most polluted sites had fewer lichens and bryophytes, so explaining a reduction in stem-scale values of alpha-diversity. This loss of species was not random however: (i) lower values of richness for competitively dominant cyano- and tripartite lichens and bryophytes would appear to curtail the development of later successional communities, while (ii) there was an absence of larger/older stems at drier and more polluted sites which had been coppiced. Each of these factors will operate additively to narrow the breadth of an epiphytic successional gradient, reducing beta-diversity and levels of species accumulation, while the absence of larger stems at coppiced sites would remove microhabitats that naturally retain the very highest levels of alpha-diversity.

The hazelwood dynamic

Allowing for the hypothesised mechanisms of species loss – lower alpha-diversity and a curtailed successional gradient – the temporal continuity of stems in close proximity in unmanaged hazelwood sites provides an important mechanism explaining the higher levels of species richness observed, and related to dispersal. Previous studies have shown that the number of epiphytes able to re-colonise trees after logging is lower than might be expected (Oldén et al. 2014), though species that are poor long-distance colonisers may be effective establishers at shorter scales within stands (Hedenås et al. 2003; Hedenås and Ericson 2008). On this basis, hazelwood stands that persist intact over long periods can accumulate a larger pool of dispersal-limited species which are then maintained because of the recurrent regrowth of stems that are closely associated over small (within-stand) distances. This would explain why old woodland indicators were unaffected by stem

size, being dependent on temporal continuity at a hazel site/stand or stool-scale, rather than the stem-scale. In contrast, coppiced hazelwood stands would lose this pool of species dependent on ecological continuity.

Coppicing may also cause species loss through changed microclimates. Old-woodland species were sensitive to canopy cover (openness), and responded negatively to more exposed habitats. This scales upwards to be consistent with the role of canopy structure (canopy cover and edge/interior environment) as a significant factor in explaining community composition and richness, though with contrasting responses across epiphytic species depending on their ecological attributes (Belinchón et al. 2007). For example, stand structure is a key factor for epiphytic bryophytes (Király and Ódor 2010) and the effect of woodland management on bryophyte communities has been related to the fact that continuous forest cover maintains local air humidity (Brunialti et al. 2010). Accordingly, Löhmus et al. (2006) showed an effect of the environment in explaining lower bryophyte cover and diversity for retention trees 2 years after logging than for trees in intact forests.

Conservation implications

Our results support the important role of Scotland's oceanic hazelwoods as the habitat for rich assemblages of oceanic mosses, liverworts and lichens in Europe. Oceanic hazelwoods form a distinct habitat that should be considered an important forest biodiversity hotspot in mainland Britain. However, in practice, *Corylus avellana* is a neglected habitat that it is not considered as a priority in the European Habitats Directive (206/105/EC November 2006). The importance of this habitat is explained by a combination of high rainfall and mild temperatures (oceanic climate), low pollution loads and low levels of human intervention which allow for the accumulation and persistence of high epiphytic diversity. In terms of underlying processes, anthropogenic effects across scales are shown to be synergistic in reducing epiphytic diversity. Thus, low values of alpha-diversity at a stem-scale are explained by pollution effects. Low compositional turnover among stems is explained by pollution (e.g. the loss of late-successional cyano- and tripartite lichens and bryophytes) and management, e.g. coppicing to curtail the stem size/age profile of hazelwood sites. There are likely to be additional effects of coppicing which affect dispersal-limited species and microclimatic specialists. Multiple factors thus reduce epiphytic diversity at a given site, and account for highly diverse relict sites in western Scotland, which have low pollution loads and complete successional gradients with broad stem size/age profiles. Furthermore, the oceanic climate of western Scotland is compatible with the occurrence of characteristic trait-groups. The relatively clean-air environment was an important factor, explaining both cyano- and tripartite lichen richness, though the oceanic climate is also likely to be significant for cyano- and tripartite lichens and a key parameter for mosses and liverworts. Cyanolichens are

strongly dependent on the amount of atmospheric moisture (Nash 2008), because they require liquid water to reactivate photosynthesis (Lange et al. 1993). In addition, mosses and liverworts are highly sensitive to moisture availability, and may decline in their occurrence/abundance at regional scales as precipitation decreases (Porley and Hodgetts 2005).

Pollution would catastrophically impact epiphytic diversity for relatively clean-air sites in western Scotland. However, in European woodland ecology, the persistence of hazel is strongly associated with coppicing. Given the role of coppicing in reducing epiphytic diversity along the impact gradient investigated here, we conclude that any intensive management of oceanic hazelwoods through coppicing would pose a significant risk to dynamics that have allowed the persistence of highly diverse niche-specialist epiphytes. Of particular importance in a European context are non-intensive traditionally managed sites, representing a compromise that protects biodiversity based on intervention that resembles natural ecosystem processes and sustains an array of native species.

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Supplemental data

Supplemental data for this article can be accessed [here](#).

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RB, BJC, RY and CJE conceived and designed the study. RB collected samples from fieldwork, identified species and analysed the data. BJC corrected the most complicated species identifications. RB, BJC, RY and CJE all contributed to writing the manuscript. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

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