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# EPIPHYTE RESPONSE TO WOODLAND HABITAT CONDITION ASSESSED USING COMMUNITY INDICATORS: A SIMPLIFIED METHOD FOR SCOTLAND'S TEMPERATE RAIN FOREST

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National vegetation classification (NVC) has been widely applied as a framework for mapping and conserving plant species and community types. However, a limited availability of expertise has prevented NVCs from being developed and used in cryptogam-dominated systems, such as for temperate and boreal epiphyte communities. This study simplified a recent systematically sampled NVC, trialled for epiphyte communities in Scotland, by reducing the original list of 82 community indicators to 34 easily recognisable species (lichens, mosses and liverworts). These were subsequently sampled from woodland sites positioned in Scotland's temperate rain forest zone. Sites were positioned among localities in less intensively managed landscapes (northwest Scotland) through to peri-urban environments (southern Scotland), grouping sites for each locality based on a contrast in woodland temporal continuity (ancient or recent). The richness and diversity of epiphyte community indicators were compared with easily measured variables reflecting stand heterogeneity or ecological stability, and woodland temporal continuity, with air pollution as a covariable. Richness and diversity were significantly explained by the ecological stability of woodland stands, heterogeneity of the light environment, and nitrogen pollution. This demonstrates a tool that can be deployed by the non-specialist, with appropriate training, to quantify the condition of a woodland stand through consequences for its epiphytes in globally important temperate rain forest. The pattern of richness and diversity was consistent with the co-occurrence of particular indicator species, which represent the range of epiphyte community types supported by a woodland.

*Keywords*. Bryophyte, community types, epiphyte sampling, lichen, woodland structure.

## Introduction

There is a long tradition in ecology of describing vegetation based on the classification of vascular plant communities (Tansley, 1913). This has strong practical value, and many countries have developed a standardised form of national vegetation classification (NVC) (Mucina *et al.*, 2000; Jennings *et al.*, 2009). Consequently, NVCs provide a basis for resource mapping including conservation assessment (Rodwell *et al.*, 1997; Dias *et al.*, 2004; Duigan *et al.*, 2007).

'Cryptogamic' groups such as lichens and bryophytes are extremely diverse as well as functionally important (Elbert *et al.*, 2012; Porada *et al.*, 2014), although many of their key habitats are neglected from NVCs; epiphytes are a case in point. Cryptogams are the

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dominant epiphytes in temperate and boreal forests. They sequester water (Pypker *et al.*, 2006a, 2006b) and growth-limiting nutrients (Reiners & Olson, 1984; van Stan & Pypker, 2015) from the atmosphere affecting forest ecosystems; they provide a critical node in trophic webs (Stubbs, 1989; Petterson *et al.*, 1995; Gunnarson *et al.*, 2004); and they add forest diversity that has unique conservation value (Coppins & Coppins, 2005; Ellis, 2016).

The gathering of information on cryptogamic epiphytes often tends towards two extremes: either citizen surveys of narrowly specified groups, such as pollution indicator guilds (Gilbert, 1974; Tregidgo *et al.*, 2013), or detailed inventory work requiring a high degree of expert knowledge (Vondrák *et al.*, 2016; Ellis & Coppins, 2017). The middle ground, in which foresters, general botanical surveyors, conservation practitioners or amateur naturalists might participate towards an informative assessment of epiphyte community status is widely lacking, although it has been successfully delivered in certain situations, including for North America (McCune *et al.*, 1997; McCune, 2000). This study aimed to develop a preliminary status assessment built around epiphyte communities in Scotland, motivated by the international importance of Scotland's lichen and bryophyte diversity and a biogeographical significance that underscores the importance of Scotland's woodlands (Coppins & Coppins, 2012; Ellis, 2016).

Examples of community classifications that could form the basis for epiphyte status assessment include the classic synecological approach of Barkman (1958), which was reinterpreted for British epiphytes by James *et al.* (1977). Both these studies were semiquantitative analyses using relevé-type methods. Additionally, a recent study in Scotland tested the potential for a systematic, quantitative inventory of epiphytes, to statistically identify and determine the relationship of community types to key habitat variables (Ellis *et al.*, 2015a). Fifteen community types were recognised and, allowing for sampling bias, thirteen of these were considered robust when critiqued by a leading field biologist (Dr Brian Coppins, Royal Botanic Garden Edinburgh, personal communication). These included a total of 82 indicator species characteristic of different epiphyte communities that occurred in Scotland's most intact native woodlands (ancient, semi-natural, minimally affected by pollution), and representing their associated habitat requirements.

Consequently, this study attempted to develop an epiphyte status assessment that is more accessible to non-specialists, by reducing the total list of community indicators provided by Ellis *et al.* (2015a) to a subset of 34 species. These are species that are representative of the different community types, and which we considered to be relatively easily recognised under field conditions (Table 1). Our aim was to provide a simplified methodology for mapping epiphyte community structure (richness and composition) that would signal an ecological response to woodland condition.

The simplified method for epiphyte survey was developed and applied to woodland sites within a single bioclimatic region: the temperate rain forest zone of oceanic western Scotland (Ellis, 2016). We compared survey results for the subset of epiphyte indicators to three effects that have been established by previous research as controlling epiphyte community structure: (i) differences in woodland temporal continuity among stands (time for colonisation) and (ii) woodland management and its effect on stand structure in terms of heterogeneity or ecological stability, while also considering (iii) large-scale pollution

Table 1. Selected indicators for contrasting epiphyte communities in Scotland, cross-referenced with previous statistical (Ellis *et al.*, 2015a) and synecological (Barkman, 1958; James *et al.*, 1977) epiphyte classifications

| Epiphyte indicator | Code | Species group (see Fig. 8) | Community type (Ellis *et al.*, 2015a) | Phytosociological analogues (Barkman, 1958; James *et al.*, 1977) |
|---|---|---|---|---|
| *Arthonia radiata* (Pers.) Ach. | Art-r | A | A: *Arthonia–Lecidella* community<br>Pioneer community on smooth bark; ± ubiquitous | *Lecanorion subfuscae* |
| *Lecanora chlarotera* Nyl. | Lec-c | A | | |
| *Lecidella elaeochroma* (Ach.) M.Choisy | Lec-e | A | | |
| *Pertusaria leioplaca* DC. | Per-l | A | | |
| *Graphis scripta* (L.) Ach. | Gra-s | A | B: *Graphis* community<br>Pioneer community, especially in oceanic climates; but with *P. occidentalis* persisting within mature smooth bark microhabitats | *Graphidion scriptae* |
| *Pyrenula occidentalis* (R.C.Harris) R.C.Harris | Pyr-o | B | | |
| *Frullania dilatata* (L.) Dumort. | Fru-d | C | C: *Frullania dilatata* community<br>Pioneer and spreading ± persistent liverwort; ± ubiquitous | *Graphidion scriptae* |
| *Melanelixia fuliginosa* subsp. *glabratula* (Lamy) J.R.Laundon | Mel-g | B | D: *Phlyctis–Ramalina* community<br>Mature community in mesotrophic habitats, especially more continental climates | *Parmelion perlatae* |
| *Parmelia sulcata* Taylor | Par-su | C | | |
| *Pertusaria amara* (Ach.) Nyl. | Per-a | C | | |
| *Ramalina farinacea* (L.) Ach. | Ram-f | Dii | | |
| *Calicium viride* Pers. | Cal-v | Dii | E: *Calicium–Chrysothrix* community<br>Veteran community; older, rough-barked leaning trees, especially continental climates | *Calicion hyperelli* |
| *Chrysothrix candelaris* (L.) J.R.Laundon | Chr-c | Dii | | |

TABLE 1. *(Continued)*

| Epiphyte indicator | Code | Species group (see Fig. 8) | Community type (Ellis *et al.*, 2015a) | Phytosociological analogues (Barkman, 1958; James *et al.*, 1977) |
|---|---|---|---|---|
| *Lecanactis abietina* (Ach.) Körb. | Lec-a | Dii | F: *Lecanactis* community<br>Veteran community; older, rough-barked leaning trees | *Calicion hyperelli* |
| *Lobaria virens* (With.) J.R.Laundon | Lob-v | B | G: *Lobaria–Normandina–Metzgeria* community<br>Mature community in oceanic mesotrophic habitats | *Lobarion pulmonariae* |
| *Thelotrema lepadinum* (Ach.) Ach. | The-l | B | | |
| *Hypnum cupressiforme* Hedw. | Hyp-c | C | H: *Hypnum–Usnea* community<br>Later successional community persisting onto older trees, especially in oceanic climates | *Usneion barbatae* |
| *Dicranum scoparium* Hedw. | Dic-s | C | I: *Hypnum–Microlejeunea* community<br>Later successional community persisting onto older trees, especially in oceanic climates | *Parmelion laevigatae* and *Usneion barbatae* |
| *Frullania tamarisci* (L.) Dumort. | Fru-t | C | J: *Frullania tamarisci* community<br>Later successional community persisting onto older trees, especially in oceanic climates | *Lobarion pulmonariae* and *Parmelion laevigatae* |
| *Lobaria pulmonaria* (L.) Hoffm. | Lob-p | B | K: *Lobaria–Isothecium* community<br>Later successional community persisting onto older trees, especially in oceanic climates | *Lobarion pulmonariae* and *Parmelion laevigatae* |
| *Parmotrema crinitum* (Ach.) M.Choisy | Par-c | Dii | | |
| *Parmotrema perlatum* (Huds.) M.Choisy | Par-p | C | | |

Table 1. *(Continued)*

| Epiphyte indicator | Code | Species group (see Fig. 8) | Community type (Ellis *et al.*, 2015a) | Phytosociological analogues (Barkman, 1958; James *et al.*, 1977) |
|---|---|---|---|---|
| *Lecanora pulicaris* (Pers.) Ach. | Lec-p | B | L: *Arthopyrenia–Lecanora* community<br>A poorly characterised assemblage but including species associated with pioneer oligotrophic habitats | Not applicable |
| *Hypotrachyna laevigata* (Sm.) Hale | Hyp-l | C | M: *Hypotrachyna–Loxospora* community<br>Mature community especially in oceanic climates and oligotrophic habitats | *Parmelion laevigatae* |
| *Mycoblastus sanguinarius* (L.) Norman | Myc-s | C | N: *Mycoblastus–Protoparmelia–Sphaerophorus* community<br>Mature community especially in oceanic to more continental climates and oligotrophic habitats | *Parmelion laevigatae* |
| *Parmelia saxatilis* (L.) Ach. | Par-sx | C | | |
| *Platismatia glauca* (L.) W.L.Culb. & C.F.Culb. | Pla-g | C | | |
| *Sphaerophorus globosus* (Huds.) Vain. | Sph-g | Di | | |
| *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksw. | Bry-f | Dii | O: *Bryoria–Ochrolechia–Parmeliopsis* community<br>Mature community especially in more continental climates and oligotrophic habitats | *Pseudevernion furfuraceae* |
| *Hypocenomyce scalaris* (Ach. Ex Lilj.) M.Choisy | Hyp-s | Di | | |
| *Hypogymnia physodes* (L.) Nyl. | Hyp-p | C | | |
| *Imshaugia aleurites* (Ach.) S.L.F.Mey. | Ims-a | Dii | | |
| *Parmeliopsis hyperopta* (Ach.) Arnold | Par-h | Di | | |
| *Tuckermannopsis chlorophylla* (Willd.) Hale | Tuc-c | Not applicable | | |

gradients as a potential confounding effect. By testing and explaining the variance in species richness and diversity, we were able to determine whether the simplified assessment of community indicators had adequate sensitivity to woodland condition, providing a proxy for epiphyte status more broadly.

## Materials and Methods

### *Field sampling*

We selected 12 regional locations (Fig. 1) distributed within the oceanic and temperate rain forest zone of western Scotland, along a putative gradient from semi-natural landscapes (northern and western) to more intensively managed or increasingly non-natural (amenity) rural or peri-urban environments (southern). Within each landscape, three woodland study sites were identified, for a total of 36 sites. These study sites contrasted in their degree of woodland temporal continuity.

1. Ancient isolated (AI): woodlands that are isolated in the landscape and have continuity $>$ 260 years (Walker & Kirby, 1989; Roberts *et al.*, 1992).
2. Regenerated isolated (RI): woodlands that are isolated in the landscape and have continuity $<$ 150 years, having no tree symbols on mid-nineteenth century Ordnance Survey first series one-inch maps (Whittet *et al.*, 2015).
3. Regenerated connected (RC): representing regenerated woodlands but connected to remnant ancient woodlands as defined by 1 and 2.

Sites were selected using a spatially explicit projection of woodland polygons (Walker & Kirby, 1989; Roberts *et al.*, 1992), to identify all RC sites $>$ 1.5 ha, and selecting those for which the other continuity classes (AI and RI) occurred within the shortest spatial distance.

Sites were surveyed from a point at the approximate centre of the woodland, using an expanding search-area approach (Fig. 2). Transect lines were followed and individual trees encountered were sampled. First, the sampled trees were scored according to their life history and structural status (Fay, 2007; Anonymous, 2008): young, mature, ancient, veteran or dead. Second, overhead canopy openness was measured at four cardinal points at 1 m distant from each tree, using a spherical densiometer (Lemmon, 1956; cf. Englund *et al.*, 2000; Paletto & Tosi, 2009); the value of canopy openness was averaged per tree. Third, the presence or absence of 34 epiphyte community indicators on the bole, up to a height of 2 m, was scored for each tree (see Table 1), with observations for any accessible branch and twig habitats.

The cumulative length of time spent on the epiphyte survey was recorded (excluding travel time between trees and environmental measurements), and survey results were grouped into 15-min intervals for a maximum search time per site of 120 min.

### *Testing epiphyte survey effort*

The richness and diversity of community indicator species were calculated for cumulative 15-min periods up to the 120-min maximum. Diversity was based on the frequency of occurrence for species, calculated among trees within each cumulative time period, and

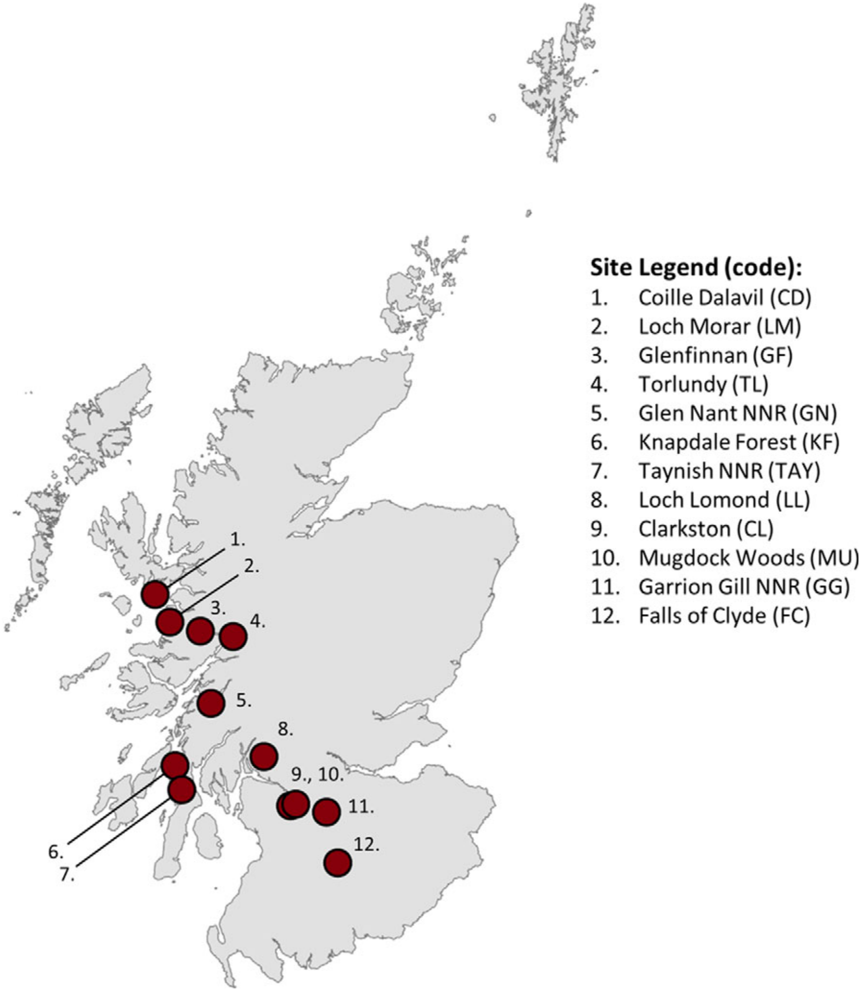

FIG. 1. Study localities (three woodland sites per locality) for the sampling of epiphyte community indicator species, along a gradient from non-intensively managed semi-natural native woodland (north and west Scotland), through to woodlands with increasing evidence of environmental disturbance (southern Scotland). NNR, national nature reserve.

used to calculate the Shannon–Wiener index, $H'$ (Krebs, 1999; McCune & Grace, 2002) in PC-ORD version 6 (McCune & Mefford, 2011). Maximum richness and diversity (at 120 min) were compared among surveys for either trunks only or including branches or twigs, to test for any survey bias emerging from the accessibility of canopy structures. To explore the degree to which a timed sampling effort affected the results, the absolute increase and percent change in richness and diversity were plotted against cumulative 15-min increments.

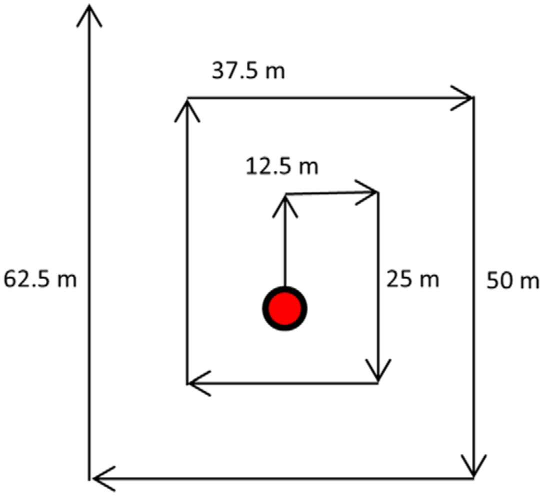

FIG. 2. Expanding search area method for the time-limited recording of epiphyte community indicators and woodland habitat condition. Trees lying within a belt that extended 2 m to either side of the transect were sampled.

### *Data analysis: species richness*

We performed exploratory analysis to understand which explanatory variables, if any, might be driving variance in indicator species richness and diversity. Accordingly, the total number of indicator species and their Shannon–Wiener $H'$ at the 120-min maximum were compared to three key effects that could be easily measured under field conditions.

1. Stand-scale effects, based on tree species, tree life-history stage and canopy structure, partitioned into measures that reflected microhabitat heterogeneity or, alternatively, the ecological stability of the stand:
    - *heterogeneity*, as the number of different tree species (including non-natives), the number of different life-history stages represented among trees, and the range of canopy openness values; and
    - *ecological stability*, as the proportion of trees that were native, the proportion of trees that were ancient or veteran, and the proportion of canopy openness values > 0.3 (chosen to represent a relatively open [mature] canopy when excluding edge effects), referenced against a representative sample of Scotland's ancient woodlands (Fig. 3).
2. Landscape-scale differences in woodland temporal continuity among the stands, whether AI, RI or RC.
3. Regional pollution gradients, as potentially confounding effects, in two forms:
    - the *total wet deposited nitrogen* (correlated with $NH_4$ and $NO_x$; $r = 0.902$ and $0.737$, $P < 0.0001$ and $P = 0.0062$ with 10 df, respectively), measured in kg $N.ha^{-1}.year^{-1}$, for the period 2004–2006 (RoTAP, 2012), and thus corresponding to a period during

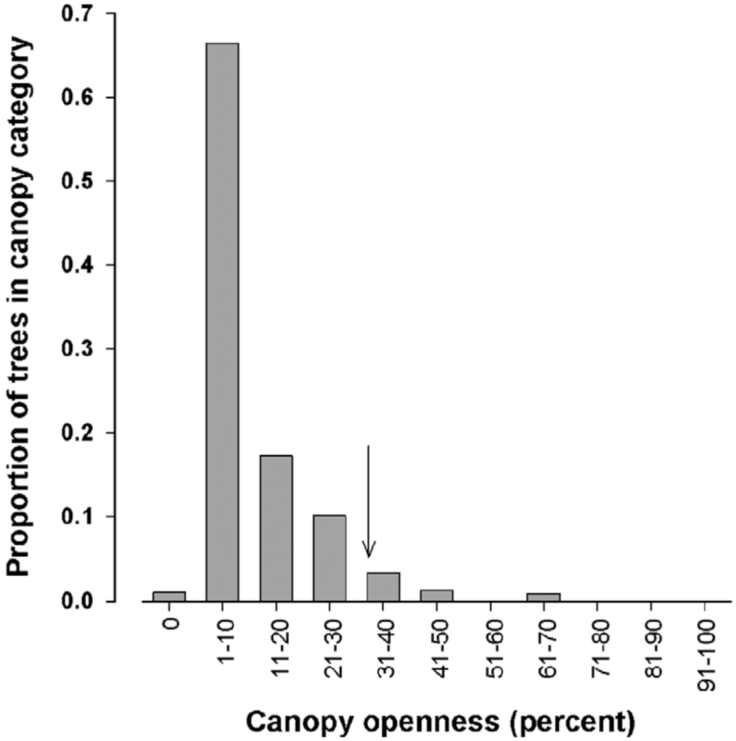

FIG. 3. Categorisation of canopy openness sampled for 250 trees across 20 ancient semi-natural, native woodlands in Scotland (Ellis *et al.*, 2015a), and the 0.3 (30%) threshold used in this study (arrow) to indicate relatively open, gladed condition.

which there has been an effect of nitrogen deposition on epiphyte distributions (Ellis *et al.*, 2014, 2015b); and

- *sulphur dioxide* *($SO_2$) concentration* in p.p.b. for the year 1987 (NEGTAP, 2001; RoTAP, 2012), and therefore testing for a potential legacy effect of past higher $SO_2$ values on epiphyte distributions (Ellis *et al.*, 2014, 2015b).

Pearson's product-moment correlation was used to explore covariance among continuous explanatory variables, and analysis of variance to compare continuous variables among categorical factors such as woodland temporal continuity. Community indicator richness and Shannon–Wiener $H'$ (both normally distributed) were compared with individual explanatory variables, using either a non-parametric Spearman's rank correlation ($\rho$) for continuous variables or a Kruskall–Wallis test ($\chi^2$) for variables treated as categorical factors.

### *Data analysis: species composition*

A pairwise comparison of site × site indicator species composition combined Bray–Curtis dissimilarity (Krebs, 1999; McCune & Grace, 2002) with frequency of occurrence values to generate a matrix, followed by two-way cluster analysis (species relativised by

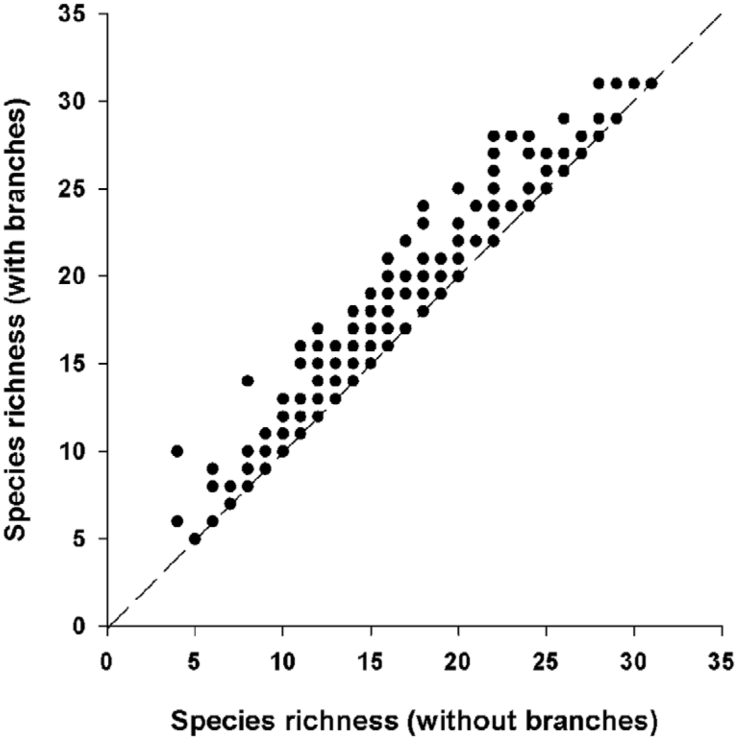

FIG. 4. Comparison of species richness per interval, among all study sites, for surveys with and without branches or twigs as a habitat component: $r = 0.969$, $P < 0.0001$ with 283 df. Values positioned above equity (dashed line) show the increase in richness with branches or twigs included.

maximum value) using flexible-beta-linkage, with beta = –0.25 (McCune & Grace, 2002), implemented in PC-ORD version 6 (McCune & Mefford, 2011). Coherent site groups, based on similarity in epiphyte composition, were visually identified from a two-way clustered heat map.

## RESULTS

We recorded 16,742 individual epiphyte occurrences from 3319 trees across the 36 woodland sites. The richness of indicator species recorded per site was correlated between the two different survey approaches with and without branch or twig components (Fig. 4), although with values higher by an average of c.1.5 species when including the additional branch habitat. Given the significant correlation, and to encourage the highest degree of standardisation among sites (i.e. comparisons among sites with different accessibility to the canopy), we refer throughout the results to the survey for trunks only (without branches). This is consistent with the original community analysis (Ellis *et al.*, 2015a).

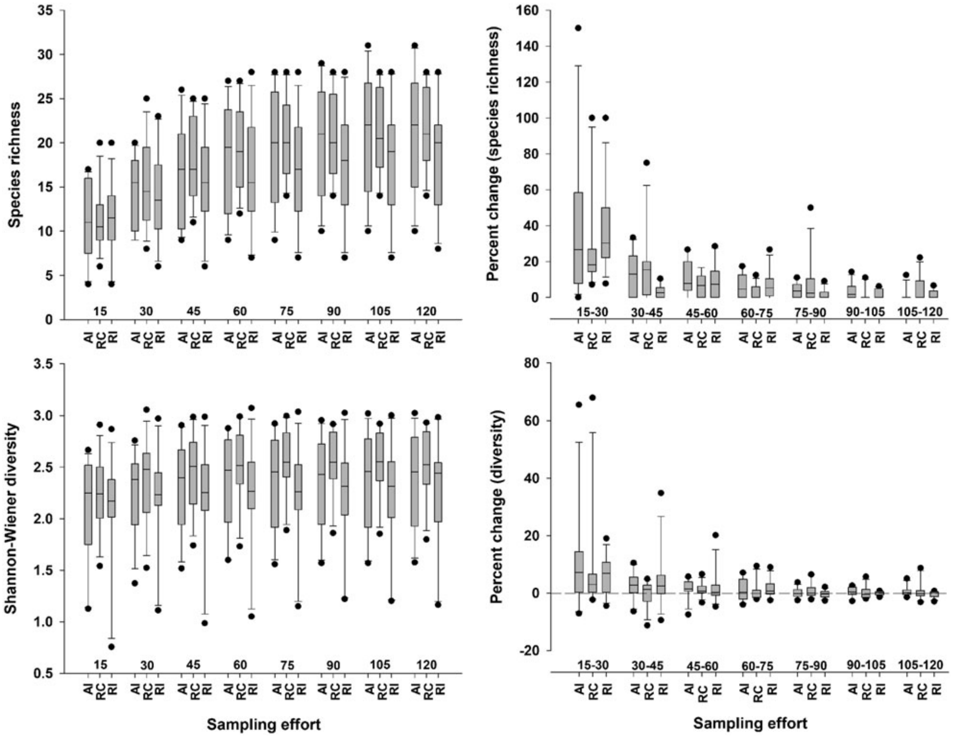

FIG. 5. Box plots to show the accumulation of species richness and Shannon–Wiener diversity ($H'$), and their percent change, for cumulative sampling periods up to the 120-min sampling time limit. Separate comparisons for ancient isolated (AI), regenerated connected (RC) and regenerated-isolated (RI) woodland sites.

On this basis, 33 of the 34 target indicator species (excluding *Tuckermannopsis chlorophylla* (Willd.) Hale) were recorded from across the woodland sites, and the species richness per site varied from 8 to 31, with a mean of 20.5 ± 5.9 (1 SD). The number of sampled trees per site ranged from 53 to 147, being lower for the most species-rich sites, because with higher epiphyte recording per tree, fewer trees were sampled during an equivalent 120-min search time. However, as a measure of survey effectiveness, the accumulating values of richness and Shannon–Wiener $H'$ declined with increasing sampling effort towards an asymptote (Fig. 5), and 120 min was considered sufficient to gain an accurate estimate of differences among sites in the epiphyte indicators, with saturation at c.60 min of sampling effort.

Explanatory variables tended to have a weak covariance structure with pairwise values of $r < 0.7$ (Table 2), except for $SO_2$ and the proportion of native trees ($r = -0.743$). However, this correlation was explained by a single site (Clarkston) with a low proportion of native trees but high $SO_2$ (21.92 p.p.b. compared with a mean of 4.19 ± 1.46, 1 SD), and there were also sites with a low proportion of native trees and low $SO_2$. There was also a

TABLE 2. Covariation among explanatory variables: comparison of continuous variables representing habitat heterogeneity, ecological stability and contrasting pollution types, using post-2000 values of total nitrogen and 1980s values of sulphur dioxide

| Variable | [1] | [2] | [3] | [4] | [5] | [6] | [7] | [8] |
|---|---|---|---|---|---|---|---|---|
| [1] No. of tree species | – | | | | | | | |
| [2] No. of life history stages | –0.056 | – | | | | | | |
| [3] Range canopy openness | –0.460** | 0.387* | – | | | | | |
| [4] Proportion native trees | –0.684*** | 0.069 | 0.337* | – | | | | |
| [5] Proportion ancient or veteran | –0.186 | 0.191 | 0.410* | 0.208 | – | | | |
| [6] Canopy openness > 30% | –0.463** | 0.055 | 0.480** | 0.237 | 0.012 | – | | |
| [7] Total nitrogen | 0.315 | –0.114 | –0.032 | –0.249 | –0.079 | –0.279 | – | |
| [8] $SO_2$ | 0.596*** | –0.133 | –0.336* | –0.743*** | –0.194 | –0.207 | 0.234 | – |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 3. Covariation among explanatory variables: comparison of continuous variables among different woodland temporal continuity categories (pollution is controlled for sites with different continuity categories)

| Variable | *F* | *P* | df |
|---|---|---|---|
| [1] No. of tree species | 0.431 | 0.654 | 2, 33 |
| [2] No. of life history stages | 0.803 | 0.456 | 2, 33 |
| [3] Range canopy openness | 0.051 | 0.951 | 2, 33 |
| [4] Proportion native trees | 1.038 | 0.366 | 2, 33 |
| [5] Proportion ancient or veteran | 4.701 | 0.016 | 2, 33 |
| [6] Canopy openness > 30% | 2.220 | 0.125 | 2, 33 |

relationship between the proportion of ancient or veteran trees and woodland temporal continuity (Table 3), and an influence of these tree- and stand-scale effects could be considered complementary (i.e. AI woodlands tended to have a higher proportion of ancient or veteran trees).

Interpreted in light of the covariance among explanatory variables (see Tables 2 and 3), both the community indicator richness (Fig. 6) and Shannon–Wiener $H'$ (Fig. 7) were significantly negatively correlated with the number of tree species (a measure of heterogeneity) and positively correlated with the range of canopy openness values (heterogeneity) and the proportion of native trees (a measure of ecological stability). Additionally, Shannon–Weiner diversity ($H'$) was positively correlated with canopy openness values > 30% (ecological stability) and negatively correlated with total wet deposited nitrogen.

Trends in species richness and Shannon–Wiener $H'$ emerged from patterns in community indicator species composition (cf. Fig. 8 with Table 1 and Fig. 1). Accordingly, four

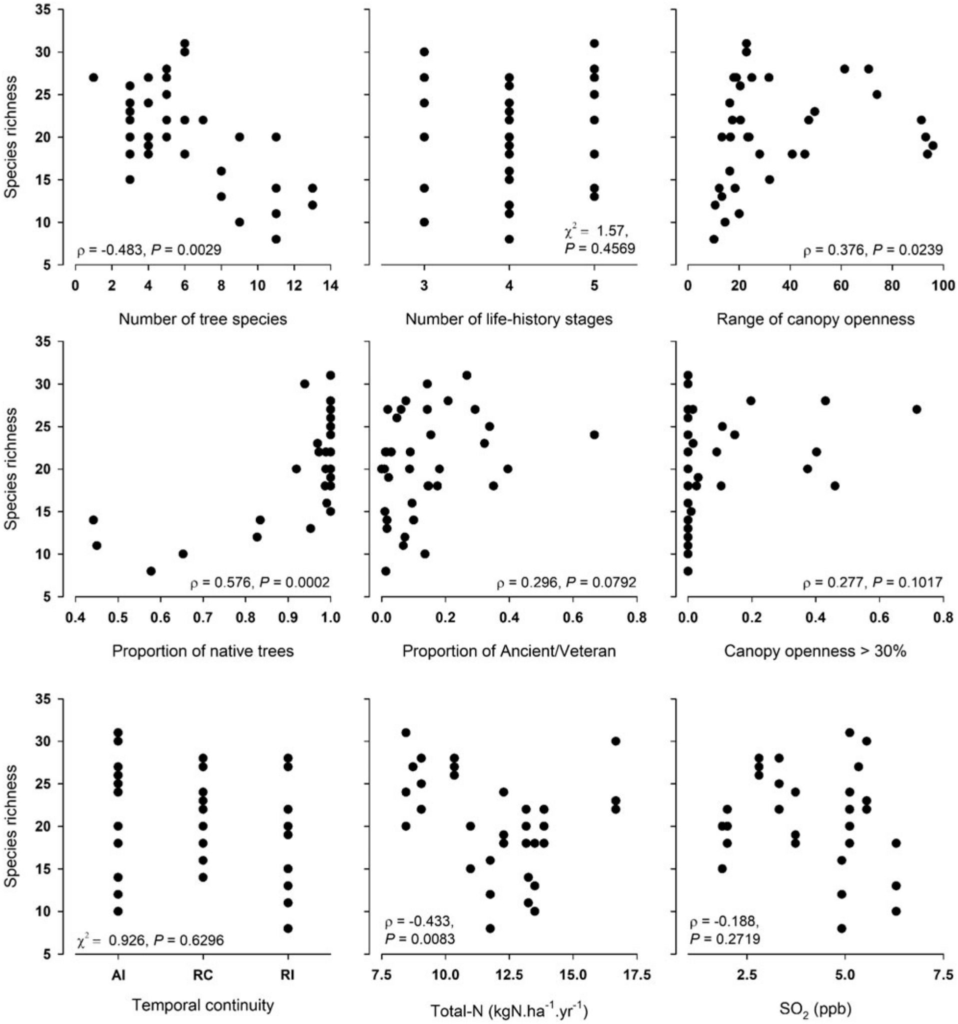

FIG. 6. Comparison of epiphyte indicator richness with putative explanatory variables. AI, Ancient isolated; RC, regenerated connected; RI, regenerated isolated.

coherent site groups were identified from the two-way clustered heat map. First, sites in group I had the fewest species and lowest diversity, and were characterised by the almost exclusive presence of pioneer species in the '*Lecanorion subfuscae*' (species group A), such as *Arthonia radiata* (Pers.) Ach., *Lecanora chlarotera* Nyl. and *Pertusaria leioplaca* DC. Second, sites in groups IIIa and IIIb had intermediate species richness and diversity, lacking pioneers but including members of the '*Parmelion laevigatae*' (species group C), signalling mature trees in humid oligotrophic environments, for example, *Hypotrachyna laevigata* (Sm.) Hale, *Mycoblastus sanguinarius* (L.) Norman and *Parmelia saxatilis* (L.) Ach. Third, sites in groups II and IV were represented by a wider range of species and

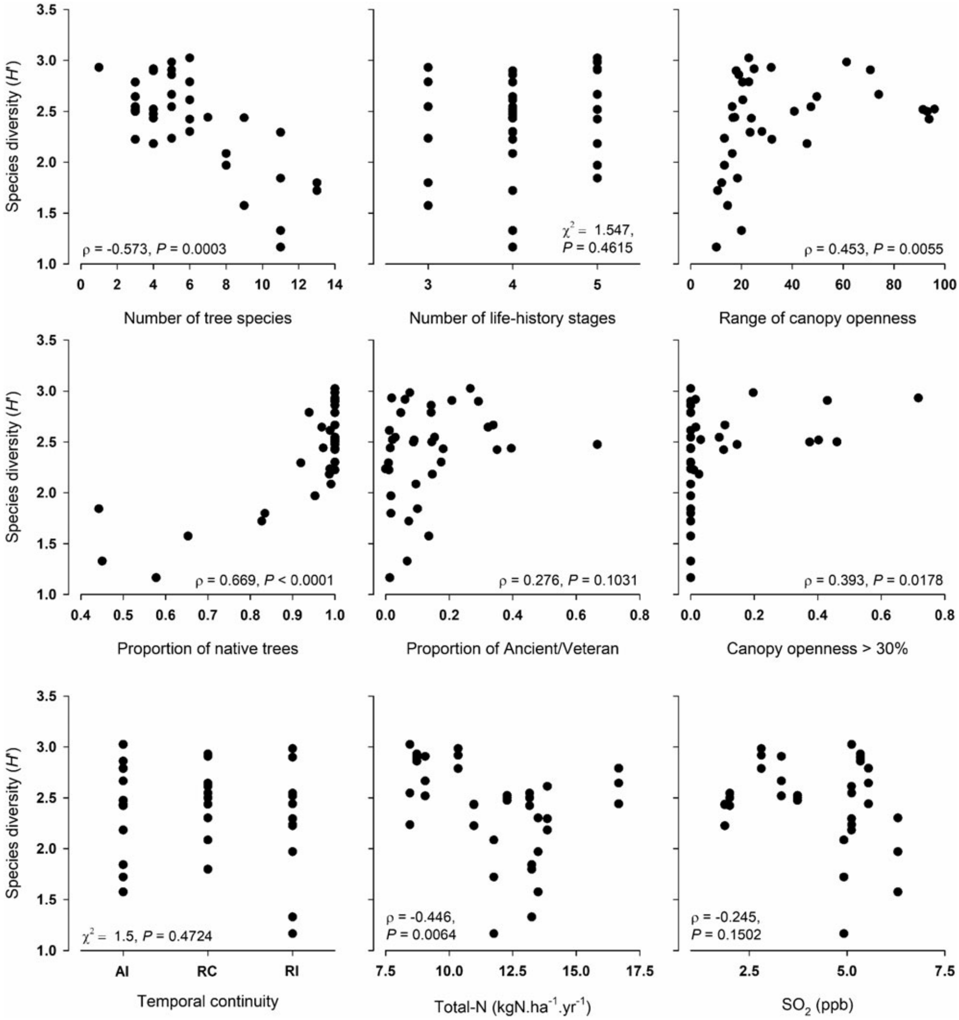

FIG. 7. Comparison of epiphyte indicator Shannon–Wiener diversity ($H'$) with putative explanatory variables. AI, Ancient isolated; RC, regenerated connected; RI, regenerated isolated.

higher diversity, including both the '*Lecanorion subfuscae*' (species group A) and the '*Parmelion laevigatae*' (species group C), but also with members of the oceanic '*Graphidion scriptae*' and '*Lobarion pulmonariae*' (species group B), such as *Lobaria pulmonaria* (L.) Hoffm., *Lobaria virens* (With.) J.R.Laundon and *Pyrenula occidentalis* (R.C.Harris) R.C.Harris. Also present were species that otherwise occurred sporadically across sites (species groups Di and Dii), and which included members of both the '*Calicion hyperelli*', for example *Calicium viride* Pers., *Chrysothrix candelaris* (L.) J.R.Laundon and *Lecanactis abietina* (Ach.) Körb., and the '*Pseudevernion fufuraceae*', for example *Bryoria fuscescens* (Gyeln.) Brodo & D.Hawskw., *Hypocenomyce scalaris* (Ach. Ex Lilj.) M.Choisy and *Imshaugia aleurites* (Ach.) S.L.F.Mey.

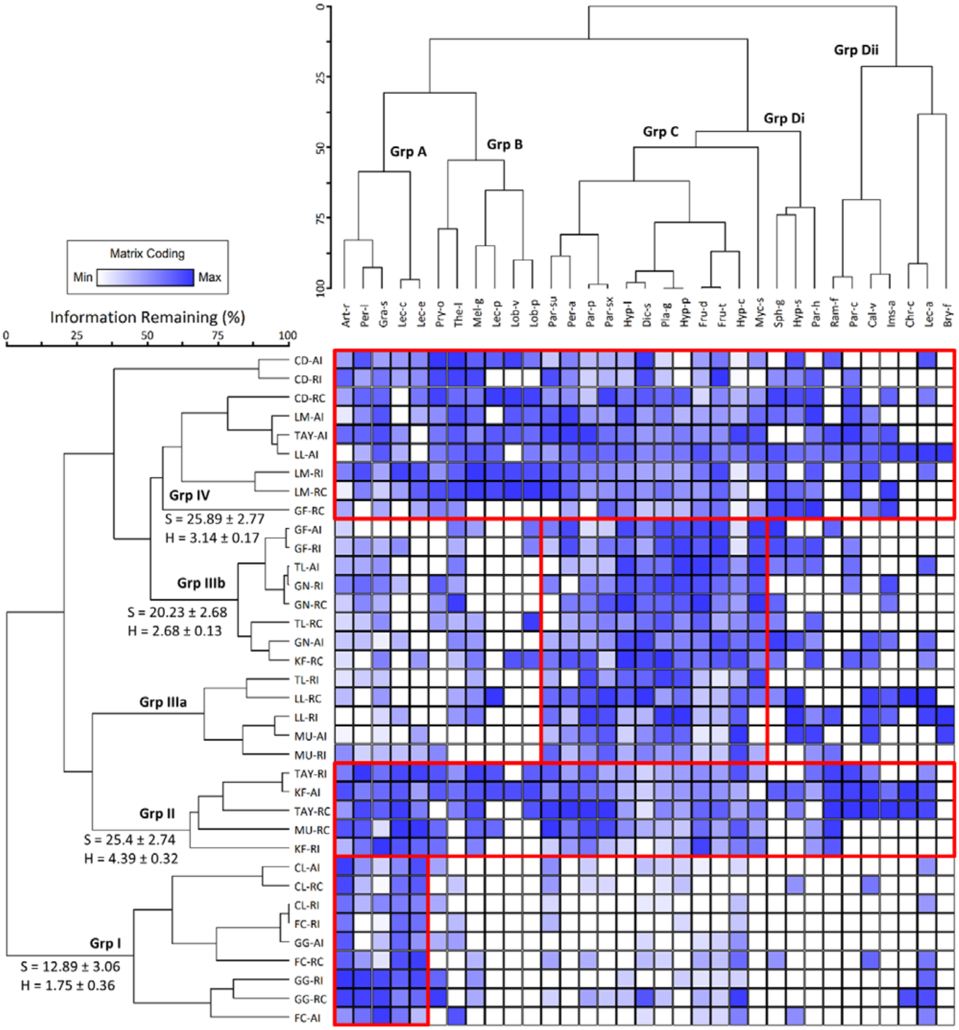

FIG. 8. Two-way clustering, with five groups used to delimit woodland site clusters (groups I–IV), and their associated assemblages of community indicator species (groups A–D). The strength of colour is determined as the percentile of each species' frequency values; two-way groupings are delimited with red boundaries. The values of species richness and Shannon–Wiener diversity (*H′*) are shown as a mean ± 1 SD for each of the woodland site clusters. Grp, group.

## DISCUSSION

Epiphytes are important to the diversity, ecosystem function and ecological characterisation of British forests and woodlands (James *et al.*, 1977; Ellis *et al.*, 2015a). Status assessment for epiphytes has been applied extensively by using a small number of easily identified indicator species suitable for citizen scientists (Seed *et al.*, 2013; Tregidgo *et al.*, 2013), or at the other extreme with greater taxonomic detail although across a limited number of sites through comprehensive inventory by specialists (Vondrák *et al.*, 2016; Ellis & Coppins, 2017). Here, we aimed to adapt the results of a systematic epiphyte survey in Scottish ancient woodland (Ellis *et al.*, 2015a) to develop a simplified method that is ecologically informative but could be applied by non-expert practitioners following a limited training period.

Our practical experience suggests that non-specialist biologists such as nature reserve managers, foresters and general naturalists could be trained to identify the 34 indicator species (see Table 1) over a weekend, although we acknowledge that misidentifications of the more difficult species (e.g. *Lecanora chlarotera* and *Lecanora pulicaris* (Pers.) Ach.) are to be expected, and that some of our species may be better considered as aggregates when recording is by non-specialists (e.g. *Parmelia saxatilis*: Corsie *et al.*, 2019). Nevertheless, the study showed that a time-limited survey of less than 2 h (45–60 min minimum) could be used to capture the richness and diversity of indicator species at a site, and because these species are drawn from different community types that associate with contrasting microhabitats (Ellis *et al.*, 2015a), results were expected to provide information about the response of epiphytes to woodland condition. Below, we discuss the interpretation of indicator trends at different scales, for pollution gradients, woodland temporal continuity, and stand-scale heterogeneity or ecological stability.

First, we found contrasting responses to pollution. Although historic $SO_2$ pollution is known to have been an important driver of epiphyte richness and diversity (Gilbert, 1970; Hawksworth & Rose, 1970), there has been a rapid and widespread decline in $SO_2$ pollution since the 1980s (Woodin, 1989; Vestreng *et al.*, 2007), with recolonisation into formerly polluted environments (Seaward, 1998). Accordingly, $SO_2$ did not correlate with epiphyte indicator trends. However, as $SO_2$ levels have declined, nitrogen pollution has increased (Woodin, 1989; Fowler *et al.*, 2004) and now affects epiphytes (van Herk *et al.*, 2003; Wolseley *et al.*, 2006). Although values of total nitrogen for the sites examined here were predominantly lower than or fell within the range of thresholds at which nitrogen starts to impact biodiversity and ecosystem function for oakwoods (i.e. 10–20 kg $N.ha^{-1}.year^{-1}$ (Air Pollution Information System, no date), there was a relationship between epiphyte indicator richness and diversity, and total wet deposited nitrogen. In particular, this can be explained by an absence of community indicators associated with oligotrophic woodland conditions (Johansson *et al.*, 2012; McMurray *et al.*, 2015), including members of the '*Pseudevernion furfuraceae*' (see Table 1: James *et al.*, 1977; Ellis *et al.*, 2015a) such as *Bryoria fuscescens*, *Imshaugia aleurites* or *Parmeliopsis hyperopta* (Ach.) Arnold.

Second, we found no strong effect of woodland temporal continuity (ancient versus regenerated sites), which has been documented as affecting epiphyte richness and diversity (Rose, 1976; Selva, 1994). However, although continuity of woodland habitat must by definition be restricted to sites in the landscape that are 'ancient' (Ellis *et al.*, 2009; Whittet & Ellis, 2013), not all ancient woodlands will preserve the old-growth condition (Lesica *et al.*, 1991; Michel & Winter, 2009) that is associated with species richness. Many ancient woodlands in Scotland have had old-growth condition managed out of them through a past process of intensive management, such as nineteenth century short-rotation oak coppice

(Smout, 2005; Smout *et al.*, 2007). Despite continuity of tree cover, this can lead to a simplification of woodland structure that negates the recurrent occurrence of old-growth niches. Furthermore, recent work in Scottish oakwoods suggests effective colonisation of old growth–dependent species from adjacent ancient (source) to regenerated (sink) sites can occur over c.50-year periods (Williams & Ellis, 2018), although with the signature of woodland temporal continuity dependent on spatial connectivity among sites. The effect size for continuity may therefore be relatively small, and hard to detect, for a limited number of sites such as those in the present study, which were not purposefully chosen to remove confounding factors, such as by controlling for local historic management or considering connectivity among sources and sinks.

Third, there was a significant effect of stand structure on epiphyte indicator richness and diversity, although with some unexpected results. For example, different epiphyte species and communities occur on different substrata, including different types of trees (Lõhmus *et al.*, 2007; Mežaka *et al.*, 2008; Spier *et al.*, 2010). Considering the well-established positive relationship between heterogeneity and species richness or diversity (Stein *et al.*, 2014), and adopting the number of tree species as a simple proxy for heterogeneity (different substrata), it is surprising that indicator richness and diversity were negatively correlated with the number of tree species in a stand. However, the number of tree species appeared to be negatively related to stand ecological stability, and was therefore increased by the occurrence of amenity non-native trees such as *Acer pseudoplatanus* L., *Aesculus hippocastanum* L. and *Fagus sylvatica* L., as well as disturbance-tolerant small tree species such as *Crataegus monogynea* Jacq. and *Sambucus nigra* L. Consequently, stands with higher numbers of different trees (in group I) were also dominated by epiphyte indicators that are considered 'ruderal' species of pioneer communities, such as the '*Lecanorion subfuscae*' (see Table 1: James *et al.*, 1977; Ellis *et al.*, 2015a). This is consistent with previous work showing a decline in epiphyte diversity linked to woodland disturbance (Aragón *et al.*, 2010; Tripp *et al.*, 2019).

As a corollary, epiphyte indicators were positively correlated with the proportion of native trees in a stand, taken as a measure of stand ecological stability. Such stands were often dominated by *Quercus* spp., with an accompanying tree species mixture including *Alnus glutinosa* (L.) Gaertn., *Betula* spp., *Corylus avellana* L., *Fraxinus excelsior* L., *Salix* spp. and *Sorbus aucuparia* L., typical of Scottish native woodlands (Rodwell, 1991; Averis *et al.*, 2004), although with some *Larix decidua* Mill. The indicator richness and diversity of these sites depended on the assembly of four compositional types.

1. Medium values of richness were achieved for sites with mature epiphyte communities (groups IIIa and IIIb), including, for example, members of the '*Parmelion laevigatae*' (see Table 1: James *et al.*, 1977; Ellis *et al.*, 2015a); however, richness was increased for situations (groups II and IV) in which stands also supported:
2. A range of contrasting mature communities, including, for example, the '*Lobarion pulmonariae*' or '*Pseudevernion furfuraceae*' associated with alternative microhabitats (see Table 1: James *et al.*, 1977; Ellis *et al.*, 2015a),

3. Older trees, which are valuable and increasingly rare components of forested landscapes (Lindenmayer *et al.*, 2012, 2014; Lindenmayer, 2017) and which enabled specialist communities on old, rough-barked and often leaning trees, such as the '*Calicion hyperelli*' (see Table 1: James *et al.*, 1977; Ellis *et al.*, 2015a),
4. Pioneer communities ('*Lecanorion subfuscae*') indicating stand regeneration.

Finally, epiphyte indicator richness and diversity were linked to canopy openness as a measure of heterogeneity in the light environment, and also being a proxy for temperature and moisture conditions. Variability in light will favour the co-occurrence of both shade- and light-tolerant species (cf. Green *et al.*, 1991; Solhaug & Gauslaa, 1996); however, the amount of open canopy was also important and is representative of old-growth gap-dynamic conditions, or alternatively 'cultural old-growth' landscapes (Bauhus *et al.*, 2009; Bergmeier *et al.*, 2010) such as in pasture woodland and ancient parkland. In general terms, lichen epiphytes (the majority of the indicator species) are physiologically sensitive to (Palmqvist & Sundberg, 2000) and limited at a community-scale (Marmor *et al.*, 2012; Nascimbene *et al.*, 2012; Király *et al.*, 2013) by available light, and during natural forest succession epiphyte richness and diversity decline during a shaded regeneration phase, increasing as canopies thin towards greater light availability (Sillett *et al.*, 2000). This effect of light availability argues in favour of traditional woodland management in maintaining open canopy conditions to support lichen epiphytes, because abandonment and secondary succession can lead to increased shading and a decline in richness and diversity (Leppik *et al.*, 2011; Paltto *et al.*, 2011).

Overall, we conclude that the relatively simple survey methods presented here can provide an effective, preliminary assessment of epiphyte community status for Scotland's woodlands. This is consistent with previous evidence that epiphyte indicators – positioned along community gradients – can be used to determine compositional turnover (McCune *et al.*, 1997), although applied here within stands to estimate indicator richness and diversity. However, we add the caveat that although richness and diversity of community indicators are proxies for the variability of community types within a site (affected by the pollution gradient, and heterogeneity and stability of native woodland microhabitats), the extrapolation to total species richness may be equivocal, especially when indicator surveys are undertaken by non-experts (McCune *et al.*, 1997; Giordani *et al.*, 2009). Moving forwards, it is desirable that this type of simple but informative method is developed to encourage wider professional engagement with epiphytic lichens and bryophytes. This should create additional demand for lichen or bryophyte surveys across sites of interest, with use of the method not precluding the need for the detailed surveys carried out by experts.

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