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Short communication

Critical tests for lichen indicators of woodland ecological continuity

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ABSTRACT

For lichen epiphytes the loss of trees from a site represents a complete break in the availability of their primary habitat. Epiphytic species are therefore expected to provide powerful indicators for the ecological continuity of woodlands. Suites of lichen indicators have been developed in a semi-quantitative way, and represent working hypotheses which are cautiously interpreted against site-specific conditions by expert field biologists. Here, we test the utility of lichen indicators in a more generic fashion, by attempting to falsify the null hypothesis that the occurrence of lichen indicators is unrelated to variation in woodland continuity. We compared the association of recommended lichen indicators with woodlands in different continuity classes, after adjusting for sampling bias. We demonstrated differences in accuracy for contrasting sub-groups of indicators related to their biogeography; a sub-group of 'western' indicators tended to be more strongly associated with long-continuity woodland compared to an 'eastern' indicator sub-group. Our results underpin the need for further research into the fundamental biology which explains the value of indicators, before these tools can be applied generally and independently of expert-led opinion in a site-specific context.

1. Introduction

Deforestation since the mid-Holocene has massively reduced the extent of primary, old-growth forest across the temperate zone, and especially in Western Europe (Hannah et al., 1995, and cf. Fig. 3.15 in the MEA 2005). Consequently, there is a strong emphasis in conservation on identifying forest remnants which retain two important ecological properties. The first of these properties is structural: the existence of key microhabitats analogous to those occurring in 'old-growth' forest stands. Examples include a unique soil quality (Verheyen et al., 1999; Wilson et al., 1997), and the greater accumulation of deadwood than might be associated with intensively managed woodland (Kirby et al., 1998). The second property is temporal: the time over which key microhabitats have persisted in the landscape, which determines the likelihood that dispersal-limited niche-specialists will successfully become established, as demonstrated for vascular plants (Brunet and Von Oheimb, 1998; Dzwonko and Loster, 1992; Matlack, 1994). These old-growth properties of (i) habitat quality and (ii) extended time-for-colonisation, form the basis of what has been referred to as 'woodland ecological continuity' (Coppins and Coppins, 2002).

Species from across a broad range of different taxonomic groups show a dependency on aspects of ecological continuity, including: invertebrates (Assmann 1999), mammals (Bright et al., 1994), lichens (Rose, 1976; Selva, 1994) and vascular plants (Peterken, 1974; Wulf, 2003). Focussing on vascular plants, it is established that sites with ecological continuity are distinctive in terms of their species composition and guild proportionality (Dzwonko and Loster, 1992; Hermy et al., 1999) with possibly greater species richness (Peterken and Game, 1984) than comparable woodland types which have a lower ecological continuity value. Given these implications for biodiversity, proxy indicators have been developed to readily identify sites with high ecological continuity and which are therefore conservation priority habitats. However, the interpretation of different indicators is dependent on the ecology of the guilds used. Vascular plant indicators may recover from extended periods of woodland degradation or even clear-felling, owing to the buffering capacity of the seed bank (Erenler et al., 2010). In contrast, epiphytes are primarily dependent on trees as their habitat substratum, and the absence of trees at a site, for example through clear-felling, represents a definitive break in species occurrence. Nevertheless, indicator groups have received general criticism as being ambiguous (cf. Nordén and Appelqvist, 2001; Rolstad et al., 2002) and in need of critical assessment. Here, we quantify the dependency of epiphytes on the continuity of tree cover to statistically test lichen indicators of ecological continuity, by drawing on the concept of 'ancient woodland' as it is adopted in the United Kingdom.

The UK's Ancient Woodland Inventory provided cartographic evidence for the time over which woodland sites have had continuous tree cover (Roberts et al., 1992; Walker and Kirby, 1987). Different categories in the temporal continuity of tree cover do not

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map exactly onto trends in ecological continuity because certain ‘ancient woodlands’, which are defined as having continuous tree cover since c. 1750, have undergone periods of historic intensive management. Despite being classed as ancient woodland, such sites may not retain high values of ecological continuity, i.e. the long-term persistence of niche-specialist microhabitats, required for the occurrence of indicator species. This may be the case for coppice Oakwood in Britain, in which the rotation of coppicing in plots on a cycle of 20–30 yr (Smout, 2005; Smout et al., 2007) will have reduced structural complexity (e.g. over-mature trees, deadwood), instigating a break in associated microhabitat persistence over long time-scales, despite continuous tree cover. Thus, not all ancient woodland sites have high ecological continuity values, conversely however, it is only from among sites with a continuity of tree cover (i.e. ancient woodlands) that the properties of high ecological continuity can be drawn, and it is these sites with which epiphytic indicator species should be significantly associated. On this basis we compared occurrence records for previously established lichen epiphyte indicators, with sites that have had continuous tree cover for different periods of time. We tested the null hypothesis of no statistical association with ancient woodland, i.e. semi-natural habitats with persistent tree cover >250 yr, relative to occurrence rates among the same indicator species for sites which are known to have undergone a period of deforestation and subsequent regeneration in the more recent past. Species for which the null hypothesis is rejected provide provisionally strong indicators of ecological continuity, as they are consistent with an expected skewness to ancient woodlands, presumably those which retain ecological continuity. Species for which the null hypothesis cannot be rejected must be treated with greater circumspection; they may have been erroneously selected as indicators, or they may not be responsive to the full breadth of ecological continuity, perhaps signalling the existence of certain niche-specialist microhabitats (which may occur outside ancient woodlands) without the additional constraint of microhabitat persistence.

Hypothesis testing using British woodlands represents a case-study region in which lichen indicators of ecological continuity were first developed (Rose, 1974, 1976), and where they have since been widely adopted in conservation assessment. However, we capture a broad problem, because among different regions the identification of ecological continuity indicator species remains largely subjective, and founded on qualitative (expert opinion) or

Table 1

Results of a chi-square test of association for lichen indicator groups (ESIEC, WSIEC, EUCIEC) with woodlands of contrasting ecological continuity: Class 1a = semi-natural since c. 1750, Class 2a and 2b = semi-natural and plantation origin since c. 1850, respectively; Class 3 = recently regenerated post-1850. The # records shows the sample size for the test (records within AWI polygons), compared to the total number of available records for the species shown in brackets. Data for the continuity classes show the observed/expected number of records, after correcting for sampling effort, which is shown as the proportion of records within each class for the generalist species. The χ^2 statistic was tested against 3 df (# classes − 1), with $P < 0.05^{*}$, $<0.005^{**}$, or $<0.001^{***}$. In addition, ecological traits are shown for each species, including different thallus growth forms (frut = fruticose, fol = foliose, squam = squamulose, crust = crustose), photobiont types (green = green-algal, cyano = cyanobacterial, tripartite = both), and reproductive strategies (sex = sexually reproducing spore-dispersed, asex = asexually reproduced diaspores dispersed by fragmentation, or by isidia or soredia).

ESIEC	Ecological traits†			Continuity class					
	Growth Form	Photobiont	Reproductive Strategy	# records	Class 1a	Class 2a	Class 2b	Class 3	χ^2
Nephroma parile	fol	cyano	asex	35 (60)	24/14.5	6/9	2/9.4	3/2.2	13.28**
Lobaria pulmonaria	fol	tripart	sex/asex	65 (121)	36/27	20/16.7	6/17.4	3/4	11.42**
Parmeliella triptophylla	squam	cyano	asex	27 (58)	11/11.2	12/6.9	1/7.4	3/1.7	10.15*
Degelia plumbea	fol	cyano	sex	22 (49)	9/9.1	10/5.6	3/5.9	0/1.4	6.15
Peltigera collina	fol	cyano	asex	47 (94)	24/19.5	12/12	6/12.6	5/2.9	5.97
Lobaria virens	fol	tripart	sex	4 (11)	1/1.7	3/1	0/1.1	0/0.2	5.39
Lobaria amplissima	fol	tripart	sex	11 (17)	8/4.6	1/2.8	1/2.9	1/0.7	5.19
Pannaria conoplea	fol	cyano	asex	19 (28)	12/7.9	4/4.9	2/5.1	1/1.2	4.20
Normandina pulchella	squam	green	asex	17 (39)	9/7	6/4.4	1/4.5	1/1.1	3.93
Sticta limbata	fol	cyano	asex	12 (32)	8/5	2/3.1	1/3.2	1/0.7	3.82
Megalaria grossa	crust	green	sex	37 (73)	18/15.3	12/9.5	5/9.9	2/2.3	3.58
Arthonia vinosa	crust	green	sex	16 (29)	10/6.6	2/4.1	3/4.3	1/1	3.16
Sticta sylvatica	fol	cyano	asex	11 (25)	6/4.6	3/2.8	1/2.9	1/0.7	1.89
Flavoparmelia caparata	fol	green	asex	4 (37)	1/1.7	1/1	2/1.1	0/0.2	1.32
Generalists:					0.415	0.256	0.267	0.062	
WSIEC									
Parmeliella testacea	squam	cyano	asex	53 (68)	41/22.1	11/23.4	1/3.9	0/3.6	28.35***
Leptogium burgessii	fol	cyano	sex	71 (160)	48/29.7	22/31.3	1/5.2	0/4.8	22.31***
Pyrenula occidentalis	crust	green	sex	81 (125)	51/33.8	28/35.8	2/6	0/5.4	18.46***
Fuscopannaria sampaiana	squam	cyano	asex	41 (73)	29/17.1	10/18.1	1/3	1/2.8	14.32**
Peltigera collina	fol	cyano	asex	77 (202)	46/32.2	27/34	1/5.7	3/5.2	12.15**
Collema subflaccidum	fol	cyano	asex	41 (109)	27/17.1	11/18.1	2/3	1/2.8	9.93*
Lobaria amplissima	fol	tripart	asex	55 (130)	34/23	15/24.3	3/4.1	3/3.7	9.24*
Pseudocyphellaria crocata	fol	cyano	asex	39 (82)	25/16.3	12/17.2	1/2.9	1/2.6	8.46*
Nephroma parile	fol	cyano	asex	52 (133)	28/21.7	19/23	2/3.8	3/3.5	3.44
Arthonia vinosa	crust	green	sex	22 (40)	12/9.2	8/9.7	0/1.6	2/1.5	2.97
Generalists:					0.418	0.441	0.074	0.067	
EUOCIEC									
Usnea filipendula	frut	green	asex	15 (37)	7/6.4	3/6.6	3/0.7	2/1.3	9.89*
Bunadophoron melanocarpum	frut	green	sex	35 (59)	23/14.9	10/15.3	0/1.6	2/3.1	8.22*
Mycoblastus sanguinarius	crust	green	sex	42 (97)	27/17.9	11/18.4	1/2	3/3.7	8.17*
Menegazzia terebrata	fol	green	asex	50 (89)	30/21.3	15/21.9	0/2.3	5/4.4	8.08*
Hypotrachyna laevigata	fol	green	asex	99 (176)	55/42.3	33/43.3	2/4.6	9/8.8	7.79
Hypotrachyna sinuosa	fol	green	asex	36 (72)	22/15.4	10/15.8	3/1.7	1/3.2	7.07
Sphaerophorus globosus	frut	green	sex/asex	94 (204)	52/40.1	35/41.1	2/4.4	5/8.4	7.07
Ochrolechia tartarea	crust	green	sex	48 (112)	26/20.5	18/21	2/2.2	2/4.3	3.14
Bryoria fuscescens	frut	green	asex	22 (37)	11/9.4	10/9.6	1/1	0/2	2.45
Generalists:					0.427	0.438	0.047	0.089	

semi-quantitative analyses (Rose, 1976; Selva, 1994; Tibell, 1992). Statistical tests in the validity of ecological continuity indicator species should therefore be considered a conservation priority.

2. Methods

We selected 29 lichen indicators of woodland ecological continuity (Coppins and Coppins, 2002: Table 1), with contrasting ecological traits (growth-form, photobiont type and reproductive mode), and which are also relatively obvious and easily identified elements of the British epiphyte flora and therefore likely to have been accurately recorded during field inventory. Site scale records of these species at 100 m resolution were downloaded from the British Lichen Society's Scottish Sites Database (http://www.thebls.org.uk/recording-mapping/bls-databases), hosted by the UK's National Biodiversity Network (http://www.nbn.org.uk/). The current suite of British lichen indicators (Coppins and Coppins, 2002) include sub-groups applied within particular biogeographic regions, distinguishing between the hyper-oceanic climate of western Scotland, and the relatively more continental north-east. We examined indicators relevant to three of these biogeographic sub-groups: (i) the West of Scotland Index of Ecological Continuity (WSIEC), (ii) the Euoceanic Calcifuge Index (EUOCIEC), and (iii) the East of Scotland Index of Ecological Continuity (ESIEC). The spatial boundaries within which a sub-grouping of indicator species is applied (WSIEC, EUOCIEC or ESIEC) were digitised as geo-referenced polygons with a c. 15 km buffer using ArcMap v. 10 (ESRI, 2010: Redlands, California). Within these boundaries, locations for the confirmed occurrence of the relevant lichen indicators were overlaid onto digitised polygons representing five woodland continuity classes, according to the UK's Ancient Woodland Inventory (AWI) (Spencer and Kirby, 1992) for Scotland (Roberts et al., 1992; Walker and Kirby, 1987): Class 1a, 'Ancient semi-natural' corresponding to woodland sites with evidence for continued existence in the landscape since at least c. 1750, with many sites possibly much older; Class 1b, 'Ancient planted origin' with evidence for continued existence in the landscape since at least c. 1750; Class 2a, 'Long-established semi-natural' with evidence for continued existence in the landscape since at least c. 1850; Class 2b, 'Long-established plantation origin' with evidence for continued existence in the landscape since at least c. 1850; Class 3 'Recent regenerated' with evidence for a break in woodland continuity (absence in c. 1850) and regeneration during the 20th Century. It was therefore possible to calculate the number of records for each indicator species associated with sites corresponding to different AWI woodland continuity classes, including those with evidence for a break in the continuity of woodland cover.

To estimate any sampling bias among AWI classes for lichen indicators, we also matched occurrence records for five common and widespread lichens with each of the AWI classes: *Arthonia radiata*, *Hypogymnia physodes*, *Parmelia sulcata*, *Pertusaria leioplaca*, and *Ramalina farinacea*. These species are not expected to be limited in their distributions by ecological continuity. The mean proportion of records for these common species, as associated with different AWI classes, was used to correct the expected number of records for each of the indicator species, that is, if their known distribution reflected sampling effort.

For each of the lichen indicator species we used a chi-square test of association to compare the expected number of records when corrected for the sampling effort in each AWI class, with the observed number of records in the equivalent class. The prior expectation was that there would be a significant association with ancient woodlands (AWI Class 1a), from which the properties of ecological continuity must be drawn (see Section 1), and fewer observed than expected records for those sites with a break in woodland cover (AWI Class 3). As an additional test, we considered lichen records from AWI Class 1 and Class 2 sites as a single grouping, representing a lower threshold for the occurrence of indicator species (woodland continuity since c. 1850) relative to an association with the Class 3 sites.

3. Results

Records for the five common and widely distributed lichen species demonstrated a bias in sampling effort away from younger secondary regenerated woodlands, towards ancient and long-established woodland sites. Approximately, 93%, 91% and 94% of species occurrences were restricted to Class 1 (ancient) and Class 2 (long-established) woodlands within the WSIEC, EUOCIEC, and ESIEC regions, respectively.

There were only two records of an indicator species from AWI Class 1b woodlands (both for *Hypotrachyna laevigata*), and this continuity class was dropped from further analysis. Correcting for sampling bias (see Methods), there were mixed results in the statistical association of lichen indicators of ecological continuity with Class 1a (ancient, semi-natural) woodlands (Table 1). For the WSIEC sub-group, c. 80% of tested species (8/10) showed a significant association with Class 1a woodland stands. This value decreased to c. 33% of tested species (3/9) for the EUOCIEC sub-group, with *Usnea filipendula* significantly associated with Class 2b sites (long-established plantations). Likewise for the ESIEC sub-group, only c. 14% (2/14) of species were associated with Class 1a woodland sites, with *Parmeliella triptophylla* significantly associated with Class 2a sites (long-established semi-natural woodlands). In a majority of cases for indicators sampled from the EUOCIEC and ESIEC sub-groups, the observed records from sites that had evidence for a break in the continuity of tree cover (AWI Class 3) was consistent with the expected number of records when corrected for sampling effort. Furthermore, there was no discernible pattern in the distribution of ecological traits for species showing a significant association with the AWI classes (Table 1), with representation across all growth forms (fruticose, foliose, squamulose and crustose), including lichens with green-algal and cyanobacterial photobionts, and with different reproductive strategies comprising sexual spore-dispersal and asexual species dispersed via larger diaspores (isidia and soredia).

Considering lichen records within AWI Class 1 and Class 2 sites as a single grouping, the association test remained significant at $P < 0.05$ (1 df) for only two species: *Leptogium burgessii* ($\chi^2 = 5.1$) and *Pyrenula occidentalis* ($\chi^2 = 5.82$), both within the WSIEC sub-group.

4. Discussion

We tested the association between lichen ecological continuity indicator species and the UK's ancient woodland inventory (see Section 1). Critically, we expected that the type of inventory data we used would be subject to a sampling bias towards perceived 'high quality' sites (Dennis and Thomas, 2000; Sastre and Lobo, 2009), which might be favoured by field recorders. We confirm that this bias existed for lichen epiphytes, which had been preferentially recorded from Class 1 'ancient' and Class 2 'long-established' semi-natural woodlands within Scotland's landscape. Fewer records from Class 3 woodlands support the underlying assumption that these sites occupy the status of secondary regenerated sites, which is not only demonstrated within the AWI classification itself, but is also consistent with the selective behaviour of field recorders. Sampling effort was inferred based on recording patterns for widely-distributed generalist species, in order to correct for bias prior to hypothesis testing.

The degree to which we rejected our null hypothesis of no association between lichen indicators of ecological continuity (Coppins and Coppins, 2002), and ancient woodland sites with known continuity of tree cover >250 yr was different among the three regional sub-groups of indicator species. Principally, there was a tendency for indicator species applied in eastern Scotland (ESIEC sub-group) to occur more frequently in Class 1a woodlands than may be expected based on sampling effort (and less frequently in Class 2b woodlands), though in a majority of cases this association was not statistically significant. This may relate to limitations in data accuracy, though we can offer several functional explanations for this discrepancy also.

The proposed indicators for ecological continuity in eastern Scotland include species which are relatively common generalists in western Scotland (e.g. *Flavoparmelia caperata*, *Lobaria virens*, *Normadina pulchella*), where they occur in woodlands across a broad range of AWI classes. It has been shown that such species may become increasingly restricted to woodlands with longer unbroken periods of continuous tree cover (AWI Class 1 ancient woodland) in a more continental and sub-optimal macroclimatic setting (Ellis et al., 2009). One plausible explanation for this effect is that woodlands with a longer continuity of tree cover include sites which are more likely to have developed or retained greater microhabitat heterogeneity, increasing the likelihood of a species' establishment into 'safe-sites' which might buffer the sub-optimal climate (cf. Ellis, 2013). However, within this niche-based interpretation, species are not necessarily dependent on the continuity of 'safe-site' microhabitats, only their occurrence, raising the possibility that while such species may tend to occur in ancient woodlands, they may also establish into younger woodland sites that have developed a threshold microhabitat structure during a single generation of larger/older trees. This role of lichen indicators in quantifying woodland habitat structure (availability of key microhabitats), as opposed to microhabitat persistence across multiple generations of trees, has been shown during previous tests of ecological continuity indicator species (cf. Ohlson et al., 1997). Rather than being indicators of ecological continuity, such species may capture the positive net effect on biodiversity of heterogeneous woodland microhabitats, analogous to the use of lichen indicators within the Scandinavian and Baltic 'woodland key habitats' concept (Timonen et al., 2010). This interpretation applies also to lichen indicator species within the EUOCIEC sub-grouping, which is again represented by species with relatively wide bioclimatic distributions.

In contrast, indicator species applied in western Scotland (WSIEC sub-group) had a strong association with AWI Class 1 ancient woodlands, evidencing skewness to those sites from which the properties of ecological continuity could be drawn. Many species in the WSIEC sub-group occur exclusively under the climatic condition of hyper-oceanicity (e.g. *Leptogium burgessii*, *Pseudocyphellaria crocata*) at the bioclimatic edge of the European landmass. The association of these species with woodlands that have a long continuity of tree cover will not be confounded by variable microhabitat specificity/availability along bioclimatic gradients, and dispersal limitation may play a more clearly defined role in their selection as indicators. These species may therefore be dependent on both microhabitat availability and its persistence, with an improved performance as ecological continuity indicators. However, where WSIEC indicators fail the test of association with AWI Class 1 ancient woodlands it is again reasonable to assume that they might operate as indicators of key microhabitat, such as for *Arthonia vinosa*, which is particularly associated with the bark or lignum of mature and over-mature trees (Smith et al., 2010), microhabitats which are not exclusively associated with ancient woodland.

4.1. Summary

We show mixed results in the efficacy of ecological continuity indicators in the British context, that is, in terms of their degree of association with ancient woodlands with unbroken tree cover, highlighting several important points. Firstly, it has been established by previous studies that indicator species are likely to have a restricted geographic scope (Sætersdal et al., 2005) and be relevant within a given habitat context (Liira et al., 2007). Additionally, we suggest that the role of putative indicator species varies between (i) those which are associated with specialist microhabitats under a sub-optimal climate, and which may occur more often within, though which are not significantly associated with ancient woodlands, and (ii) those species which are accurate indicators of ecological continuity through a dependency on the long-term persistence (across multiple generations of trees) of specialist microhabitats.

Secondly, it will be important to expand the scope of existing research to consider individual woodlands not simply as discrete entities, but within a woodland site network (cf. Bailey, 2007; Johansson et al., 2012) that includes habitat quality and connectivity within the wider landscape. This would expand on our preliminary analyses by allowing indicator species to be interpreted within a broader landscape context, the structure of which will influence their suitability in identifying sites with high ecological continuity.

Thirdly, if ecological continuity indicator species are to form a more general framework in conservation, e.g. for the prioritisation and management of habitats for protection, then it is critically important to understand the extent to which the component species are constrained in their distributions by microhabitat availability (niche specialists), or time-for-colonisation (dispersal-limitation), or both (cf. Fritz et al., 2008). The results from this study concur with previous work in demonstrating that *Lobaria pulmonaria* may operate as an indicator species outside the oceanic climate zone (Campbell and Fredeen, 2004), possibly explained by dispersal limitation (Öckinger et al., 2005), and related in some way to the niche-demands of cyanobacterial or tripartite associated lichens (Kuusinen, 1996; Ellis, 2013). Evidence from *L. pulmonaria* has supported contrasting high and low dispersal rates and patterns of gene-flow for sexually-reproducing and asexually dispersed lichens, respectively (Werth et al., 2006; Jüriado et al., 2011). However, across the full suite of species examined we found no clear link between lichen growth form, photobiont association or reproductive mode, and the status of a species as an ecological continuity indicator. This points to a difficulty in generalising broad ecological processes based on easy to measure phenotypic characters.

Finally, and in conclusion, our study highlights the fact that lichen indicators of ecological continuity represent working hypotheses developed by expert field biologists, which are often cautiously interpreted on the basis of local site context; their indiscriminate use should be avoided. As it stands, lichen indicators of ecological continuity may identify valuable habitat for protection, though they lack a sufficient functional biology required for a robust ecological interpretation of habitat dynamics to inform conservation.

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