



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.

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

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