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The cryptogamic epiphytes of ash (*Fraxinus excelsior* L.) in an ancient pasture-woodland: relationships with some environmental variables of relevance to woodland epiphyte management

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Abstract – One hundred and fifteen species of epiphytes were recorded from 75 ash trees in an ancient pasture-woodland along with nine environmental variables. Significant positive correlations were obtained between species richness and three of these: girth, canopy width and exposure. Total epiphyte cover also correlated positively with girth. Overall, microlichen cover>bryophyte>macrolichen cover. The largest trees possessed the largest number of 'old forest' taxa but no well-defined associations were observed. Proximity of trees to open water also influenced the occurrence of some species. Bark analysis from a subsample of trees showed that calcium was positively correlated to girth and total phosphorus negatively correlated, demonstrating the complexity of tree-epiphyte relationships.

The study confirms the importance of ash as a phorophyte for a wide range of cryptogamic epiphytes and emphasises the need for conservation measures in the wider context of woodland management, with the provision of open glades on different scales permitting a broad range of exposure and sheltered habitats plus a sustainable age-structure for the tree population to help stabilise woodland diversity.

Bryophytes / lichens / epiphytes / exposure / species richness / bark / chemistry

INTRODUCTION

The ash (*Fraxinus excelsior* L., Oleaceae) is a common indigenous tree of the United Kingdom (Wardle, 1961) growing on fertile soils in areas of moderate to high precipitation. It occurs in most of Europe, extending from about 64°N to the Mediterranean and North Africa. Its northern limit is set by cold intolerance and it is most abundant over calcareous rock or on base rich soils. Ash is long-lived and may attain large dimensions (girth up to *ca* 6 m, age to *ca* 350 yr). Cryptogamic ecologists have long been aware of its importance as a host for a wide range of epiphytic bryophytes and lichens (Moe & Botnen, 1997; Gilbert, 2000; Smith, 2004). In the UK it supports a number of "old forest" cryptogams, notably the large cyanolichens and other members of the *Lobarion* community that have been declining in Europe over past decades (Rose, 1988; Bates, 1992;

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Walser *et al.*, 2002). Old trees, particularly pollards may carry in excess of fifty species of cryptogamic epiphytes, a number that is rarely exceeded on any other European tree species. The conservation and management of ash is therefore of particular importance.

Ancient pasture-woodland is a valued, high-diversity habitat in the UK (Ferris & Humphrey, 1999; Sanderson & Wolseley, 2001) whose conservation for biodiversity is a major concern. Woodland management is necessary for the maintenance of this biodiversity and the monitoring of cryptogamic epiphytes provides one means of measuring the success of management methods and optimising future management strategies.

Although there have been significant advances in our knowledge of cryptogamic epiphyte ecology over the past decades (Ihlen *et al.*, 2001; Ellis *et al.*, 2009; Morley & Gibson, 2010) the processes leading to succession and composition remain poorly understood. While progress has been made in elucidating the effects of radiation and water relations (e.g Bates, 1992; Ellyson & Sillett, 2003) the influence of the substratum, particularly in relation to nutrient uptake and turnover has been little investigated. The use of cryptogamic epiphytes as indicators of forest biodiversity has also received much attention. They can be examined rapidly at any time of year, respond quickly to environmental change and show relationships with other organisms such as invertebrates (Petterson *et al.*, 1995).

The aims of the study are threefold: a) to seek relationships between species richness of ash epiphytes with a range of local environmental variables in an area of ancient pasture-woodland southern England: b) explore patterns of change in cryptogam cover in relation to these variables; c) outline a strategy for ash management sympathetic to the maintenance of a high cryptogamic diversity.

METHODS

The study area was located in a region of ancient park-woodland approximately 600 ha in area 5 km south of Tunbridge Wells, West Sussex (51.08°N, 0.16°E]. Bedrock consisted of soft Cretaceous sandstones and clays overlain by moderate to thick brown forest soils supporting predominantly oak-ash woodland with an understorey of *Crataegus monogyna* and *Ilex aquifolium*. The terrain was dissected by a dendritic drainage system into locally deep valleys but rock exposures were rare. Mean annual air temperature was 10.4°C and total annual precipitation close to 1000 mm.

Seventy five trees were selected in order to obtain an approximately even distribution of girths and as good a spread of locations within the area as possible (Fig. 1). Owing to the scarcity of old trees, only a small number with girths exceeding 4 m could be examined.

Community variables

All cryptogam species, excluding microalgae and fungi were listed from tree base to a height of 2.1 m on the stem of each tree. For critical taxa, small samples were removed so that identification could be confirmed under the microscope. A pilot study established that careful scrutiny and estimation over percentage cover by eye was the most efficient method of obtaining quantitative estimates (cf. Rose, 1976). For stems exceeding 1 m in girth, 30 minutes was

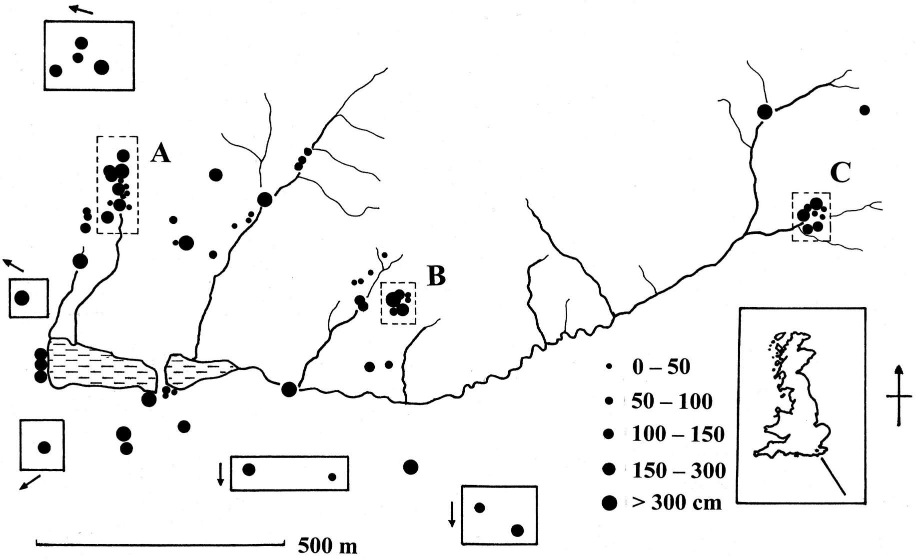

Fig. 1. Ash tree locations within the study area. Trees situated within solid rectangles with direction arrows were located outside the area of this map. Clumps within the broken rectangles A,B, C are discussed in the text.

adequate for a detailed investigation of percentage cover of taxa. For each tree five community variables were measured: species richness; total cryptogam cover; bryophyte cover; macrolichen cover and microlichen + *Trentepohlia* algae cover. Shannon and Simpson diversity indices were also calculated but they correlated strongly with species richness ($r = 0.8$, $p < 0.0001$; $r = 0.63$, $p < 0.0001$ respectively) and were not used further in the analyses.

Environmental variables

A series of eleven environmental measurements were initially made at each site: 1) tree altitude using satellite navigation equipment; 2) girth at 1.3 m height; 3) surrounding tree density using a relascope (Holgate, 1967); 4) TOPEX (Pyatt *et al.*, 1969), an estimate of the angle subtended from the horizon to the zenith at the eight cardinal compass points; 5) evergreen cover, estimated as a percentage of the 360° sweep around the tree to a distance of 50 m; 6) shrub density; relative ground cover around the tree to a distance of 20 m; 7) width of the tree canopy; 8) number of other ash trees occurring within a radius of 50 m; 9) number of large trees (girth > 3 m) occurring within a radius of 200 m 10) distance to nearest open water (streams and ponds); 11) average length of continuous woodland cover from the tree in the four cardinal compass points termed “forest depth”. This last was determined using large-scale maps. Shrub density was estimated by counting stems less than 5 cm in diameter at their base to a distance of 20 m. Counts were centred on the four compass points and complemented the relascope measurements used for tree diameters > 5 cm.

Three of the above measurements were used to construct an index of light and wind exposure for each tree. A weighted index of light exposure

(Pentecost & Richardson, 2011) was used to compare sites. It is based upon three of the environmental measurements. The TOPEX values described above were modified using an aspect-weighting so that south-facing values received a higher score than north-facing values by a factor of 1.75 (Pentecost & Zhang, 2006). The weighted values were then summed over the eight cardinal points and expressed as a percentage (T) of the maximum possible value. These were added to the relascope measurements (R), suitably adjusted so that high values represented high exposure:

$$R = 100 - (M_t/M_{max} \times 100)$$

where M_t is the relascope measurement recorded at the site and M_{max} is the maximum relascope value obtained in dense forest. Finally these were added to the percentage of the 360° sweep that was clear of evergreen cover (E). For example, suppose T (the weighted TOPEX) was calculated as 75%, R as 37% and E as 95%. Then $R + E + T = 207$. The maximum value of this sum is 290, so the index expressed as a percentage is $207/290 = 71\%$ representing a moderately exposed site. In common with light, wind exposure will be dependent upon local topography and density of tree cover. These aspects are covered by the factors R, E and T so the above measure is also an indicator of wind exposure. Since the exposure index embodied the relascope values, TOPEX and evergreen cover, these were excluded from the statistical analyses so that a total of nine environmental variables were used.

Bark chemistry

Clean surface bark samples were taken to a depth of c. 3 mm from 24 of the ash stems at a height of 1.3 m in areas where epiphytes were absent. Bark surface pH and conductivity was determined on sieved and ground samples (van Herk, 2001). Soluble tannins were determined on the same extract by measuring absorbance at 450 nm in 10 mm cells. Total phosphorus was determined by the method of Andersen (1976) followed by total Ca using EDTA titrimetry (Eaton *et al.*, 2010).

Statistical analysis, ordination and nomenclature

For bivariate analyses, Spearman rank correlations were undertaken between the community and environmental variables. A multivariate analysis (Canonical Correspondence Analysis, CCA) was undertaken using a reduced data set using 50 of the 75 sampled trees and the 28 most frequently encountered species (ter Braak, 1987) using the Canoco 4 program (ter Braak & Smilauer, 1998). A Power transform was implemented on the raw exposure data to normalise the frequency distribution. The data set was reduced in size to permit a clearer interpretation of the resulting biplots. Species names and nomenclature follow Smith *et al.* (2009) for lichens, Hill *et al.* (2006) for mosses, Söderström *et al.* (2007) for liverworts and Stace (1991) for vascular plants.

RESULTS

Community variables and environmental variables

Intercorrelations between the nine environmental variables are shown in Table 1. Owing to the size of the table, correlations with $p > 0.005$ were not deemed significant. Tree girth is seen to be significantly positively correlated to both canopy width and the exposure index and negatively correlated to the same tree count. Otherwise the only other strong correlation ($p < 0.001$) is between forest depth and number of large trees.

Table 1. Spearman rank correlations between the nine environmental variables

	Girth	*Canopy width*	*Exposure*	*Same tree*	*Large trees*	*Shrub*	*Forest depth*	*Open water*	*Altitude*
Girth									
Canopy width	** **.847**								
Exposure	** **.561**	** **.501**							
Same tree	** **–.521**	** **–.543**	** **–.400**						
Large trees	* **–.278**	ns	ns	* **.352**					
Shrub density	ns	ns	ns	ns	ns				
Forest depth	ns	ns	ns	ns	** **.394**	ns			
Open water	ns	ns	ns	ns	ns	ns	ns		
Altitude	* **–.245**	* **–.244**	ns	ns	ns	ns	ns	ns	

** $p < 0.001$; * $p < 0.005$; ns indicates $p > 0.005$.

Means and ranges of the environmental variables are shown in Table 2. Relationships between five community variables and environmental variables are presented in Table 3. Strong positive correlations were obtained for these community variables and girth with the exception of lichen cover. Thus the larger trees had a more species-rich epiphyte flora and a greater cover, the latter mainly attributed to the bryophytes. The strongest correlation was between girth and species richness.

An almost identical pattern occurred between canopy width and the community variables, although girth and canopy width were inter-correlated. Tree exposure was also strongly positively correlated with species richness, but not at all with cover, indicating that species numbers rather than their relative abundance was affected. The presence of large trees, which were mainly a mixture of oak (*Quercus robur*), beech (*Fagus sylvatica*) and ash within a 200 m radius of the study sites did not appear to influence the cryptogam community with the exception of a significant negative correlation with bryophyte cover. However, as the local density of ash trees increased, it is apparent that cryptogam species richness declined significantly along with bryophyte cover.

Table 2. Means and ranges of the 9 environmental variables

Variable	*Mean*	*Range*
Girth cm	164	14-568
Canopy width m	5.47	1.2-16
Ash density	16.3	0-86
Large trees in 200 m radius	23.3	1-59
Shrub density	67	0-151
Mean forest depth over 4 cardinals m	699	0-1188
Exposure index %	80.0	48.7-94.2
Altitude m	98	70-145
Open water proximity m	42	0-260

Table 3. Spearman rank correlations between the community and environmental variables for the 75 ash trees. Codes as for Table 1

	Total cover	*Bryophyte cover*	*Macrolichen cover*	*Microlichen cover*	*Species richness*
Girth	** .428	** **.510**	ns	ns	** **.691**
Canopy width	** .480	** **.526**	ns	ns	** **.595**
Exposure	ns	ns	ns	ns	** **.547**
Ash density	** -.364	** **–.479**	ns	ns	** **–.436**
Large trees	ns	** **–.403**	ns	ns	ns
Shrub density	ns	ns	ns	ns	ns
Forest depth	ns	ns	* **.354**	* **.286**	ns
Open water	** -.391	ns	ns	* **–.336**	ns
Altitude	ns	ns	ns	ns	ns

The presence of open water also appears to have had a negative influence on cryptogam cover, particularly among some microlichens. Finally, as forest depth increased, the lichen cover decreased to some extent, but total species richness was not affected. Shrub density and site altitude had no measurable effect on the community variables.

Species richness is plotted against girth in Fig. 2. This measure showed a non-linear relationship with girth. A rapid increase occurred until girth attained 1 m after which the rate of increase declined. The largest tree, with a girth of 5.68 m was estimated to be about 300 years old based upon tree coring, and hosted 33 epiphyte species.

Further information on cryptogam species richness and cover is shown in Table 4. It demonstrates that individual trees can support a large number of epiphyte taxa, that the lichens contribute more to species richness than the bryophytes and that microlichens and bryophytes are more important in terms of cover than macrolichens. Statistics relating to diversity indices and evenness are included for information only.

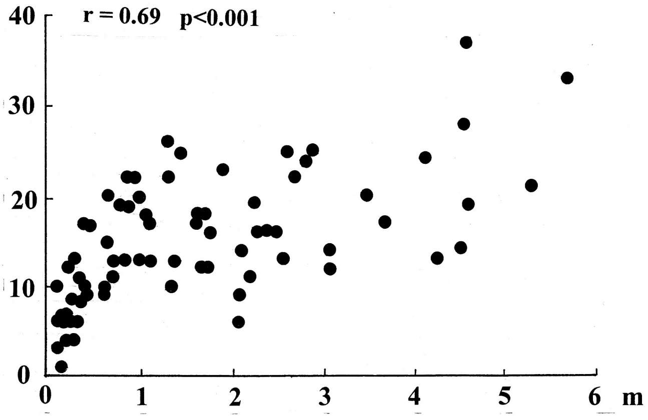

Fig. 2. Relationship between epiphyte species-richness and tree girth (m) with Spearman rank correlation coefficient.

Table 4. Means and ranges for some cryptogam community variables on ash. The range for species richness refers to numbers on individual trees

Variable	*Mean*	*Range*
Total species richness	14.9	1-37
Shannon diversity index	1.61	0-2.68
Shannon evenness	0.61	0-0.96
Simpson diversity index	3.93	1-11.2
Macrolichen richness	3.2	0-9
Microlichen richness	7.2	1-22
Bryophyte richness	4.1	0-12
Cryptogam total cover, %	42.8	0.5-96
Macrolichen cover %	3.3	0-40
Microlichen cover %	17.1	0.1-60
Bryophyte cover %	14.0	0-62

Flora

A total of 115 cryptogam taxa were identified on the 75 trees (21 mosses, 6 liverworts, 86 lichens, 1 fern and 1 alga). Although other algae were present, only visually evident *Trentepohlia* was recorded. One vascular epiphyte was found, *Oxalis acetosella*. The twelve most abundant cryptogams in terms of cover and frequency on the tree boles are listed in Table 5. A list of the remaining 103 species with their estimated cover and frequency are placed in the appendix.

Eight bryophytes, 24 lichens and the fern were recorded from only a single tree and the number of taxa recorded on less than 8 of the 75 trees was 71, of which 54 were lichens.

Table 5. Cover and (frequency) estimates of twelve most common epiphytes in descending order of cover

Taxon	*% Mean cover (frequency as % of trees with taxon present)*
Trentepohlia abietina	8.3 (48)
Hypnum cupressiforme	3.4 (49)
Lecanora expallens	2.4 (51)
Kindbergia praelonga	1.9 (41)
Metzgeria furcata	1.7 (48)
Hypnum resupinatum	1.7 (67)
Isothecium myosuroides	1.6 (29)
Enterographa crassa	1.3 (17)
Lepraria incana agg.	1.2 (76)
Parmelia sulcata	1.1 (52)
Brachythecium rutabulum	1.1 (43)
Lecanora cf. *jamesii*	1.1 (17)

Succession

To identify succession, trees were divided up into five girth categories: 0-50; 50-100; 100-150; 150-300 and > 300 cm containing approximately equal numbers of trees and the presence or absence of taxa identified. Twenty four taxa were present in all categories (7 bryophytes, 8 macrolichens, 9 microlichens), the most abundant being *Kindbergia praelonga*, *Hypnum cupressiforme*, *Phlyctis argena* and *Lepraria incana* agg. Species present only on the youngest category (0-50 cm) were all microlichens, but only *Fuscidea lightfootii* was common. Taxa present only on the three youngest categories totalled 19 (5 bryophytes, 2 macrolichens, 12 microlichens) but the only frequent species were *Ulota crispa*, *Hypogymnia physodes* and *Mycoblastus fucatus*. The oldest two categories containing mature and veteran trees > *ca* 50 years old (150-300, > 300 cm) had a total of 41 species that were not present on the younger trees (one fern, 10 bryophytes, 5 macrolichens and 27 microlichens). They included several “old forest” lichens (Rose, 1976), e.g. *Leptogium lichenoides* and *Punctelia reddenda* but only seven old forest taxa were found on more than three of these older trees: *Homalothecium sericeum*, *Catinaria atropurpurea*, *Chrysothrix candelaris*, *Enterographa crassa*, *Gyalecta truncigena*, *Lecanactis abietina* and *Schismatomma decolorans*. Nineteen taxa exclusive to the younger trees (first three girth-categories) were “replaced” by 41 taxa confined to the two oldest groupings. *Leptogium lichenoides* was the only cyanolichen recorded on any of the trees. The differences encountered on trees of different girth could be related to the larger area of bark present on the older trees permitting a greater chance of their being discovered, but a larger, more general survey, conducted on several hundred trees at this site suggests that the ‘older tree group’ listed above is not a statistical artefact and these species really are only present on the larger trees.

Cover of the pleurocarpous mosses increased significantly with tree girth ($r = 0.28$, $p < 0.05$) and this increase was due mainly to one species, *Hypnum resupinatum*. Cover of hepatics did not increase significantly with girth, but with microlichens there was ($r = 0.57$, $p < 0.001$).

With reference to Fig. 1, it is evident that the sampled trees were distributed non-randomly within the study area, many occurring within clumps. Analyses of the flora from clumps A-C (Fig. 1) showed that some taxa, although apparently indifferent to tree girth, were more frequent than expected within particular clumps. Using numbers in parentheses to indicate the ratio of the frequency within the clump to the average frequency obtained from all 75 trees it was clear that: *Pertusaria albescens* (8) within clump A; *Flavoparmelia caperata* (3) and *Parmotrema perlata* (3) in clump B and *Arthonia spadicea* (3) and *Trentepohlia abietina* (2) in C were considerably more frequent than the average. The cause might be the result of local dispersal of propagules between trees.

Multivariate analysis

Seven of the nine environmental variables were used in the analysis since canopy width was strongly correlated to girth and altitude was uncorrelated with any community variable. The results are displayed in Figs 3 and 4. The eigenvalues of the first four axes were 0.328, 0.152, 0.127 and 0.093 and totalled 84% of the species-environment variation. Since the first two axes accounted for the majority of the variation (58%) only these were used in the ordinations.

The biplots confirm to some extent, the results of the intercorrelations: tree girth (age) had a strong influence on the composition of the flora (Fig. 3), and was opposed to ash density possibly reflecting the association of young trees in some of the clumps. An influence of forest depth and large trees was apparent and these appear to be related, suggesting that larger trees occurred deeper within the wooded area. The effect of exposure was less apparent and opposed to the occurrence of large trees, presumably due to canopy shading effects. The species ordination (Fig. 4) indicated a main cluster of taxa surrounded by a few outliers. There were no obvious species groupings. Among the outliers, *Opegrapha varia* (Opv) is a species characteristic of dry shaded bark. The moss *Thamnobryum alopecurum* (Tha) was not common but tended to occur on the older trees associated with a higher than average shrub density, and the pleurocarp *Homalothecium sericeum* (Hos) was more common on trees that were moderately exposed. Crustose lichens *Opegrapha vulgata* (Opu) and *Porina aenea* (Poa) were strongly associated with water proximity suggesting a requirement for continuous high humidity. The sorediate lichen *Phlyctis argena* (Pha) occurred in small quantity on most of the trees with a tendency for greater abundance on the younger boles. This lichen contained the alga *Trentepohlia* as phycobiont and the distribution of free-living *T. abietina* (Tra) showed a similar trend, becoming scarce on the older trees. It is evident that despite that fact that the old forest lichens were confined to larger trees, no well-defined associations of cryptogams were detected.

Bark chemistry

Summary data for the analysis of 24 bark samples are shown in Table 6. There were large variations in some constituents, notably pH and soluble tannin content where the range exceeded an order of magnitude. Significant trends with girth were found only for calcium and phosphorus (Fig. 5). For calcium there was a significant positive correlation with girth ($r = 0.695$, $p < 0.001$) ranging from about 1% dry weight on the smallest trees to about 5% on the largest. The relationship is linear for trees with a girth below about 1.5 m but it becomes more

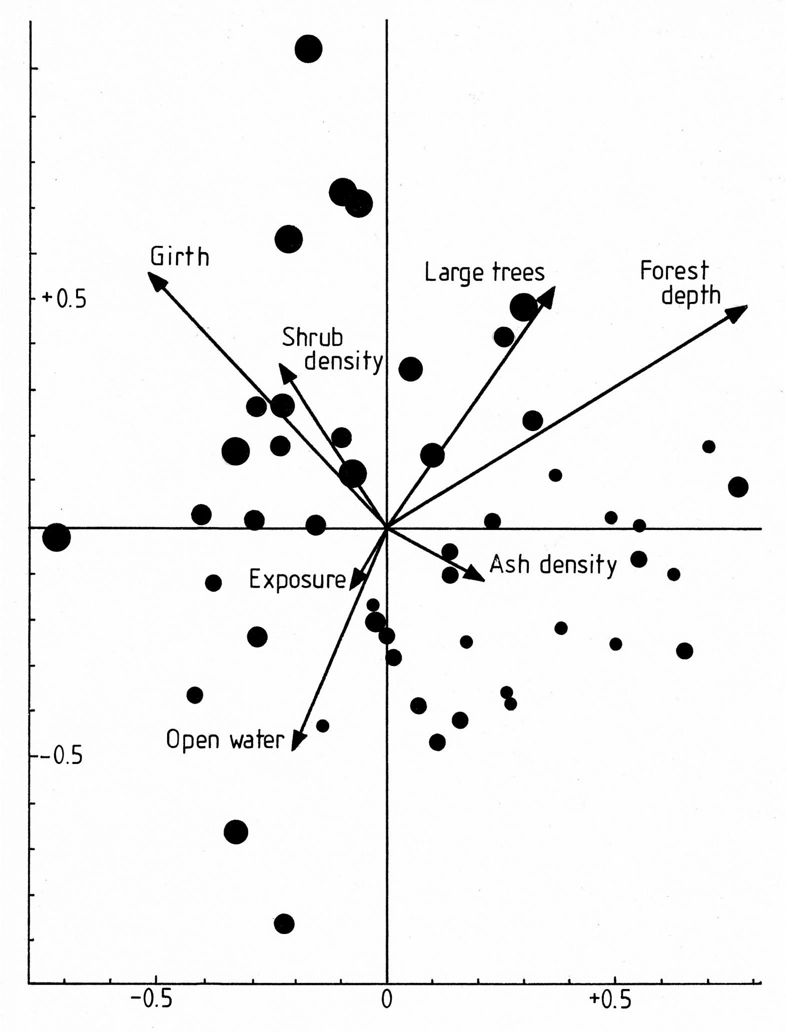

Fig. 3. Canonical community ordinations for a reduced data set (see text for details): Ordination of a subset of 50 ash trees with seven environmental variables. Tree girths were placed in five size classes indicated by dot sizes. Axes 1 and 2 of the ordination parallel to the ordinate and abscissa respectively.

variable on the larger trees. The phosphorus content of the bark was negatively correlated to girth ($r = -0.61$, $p = 0.003$) and ranged from about 0.05% dry weight on the smallest trees to 0.01% on the largest, and phosphorus levels did not decline greatly as girth increased above 2m. There was only one significant intercorrelation, that between bark pH and conductivity ($r = 0.97$, $p < 0.01$).

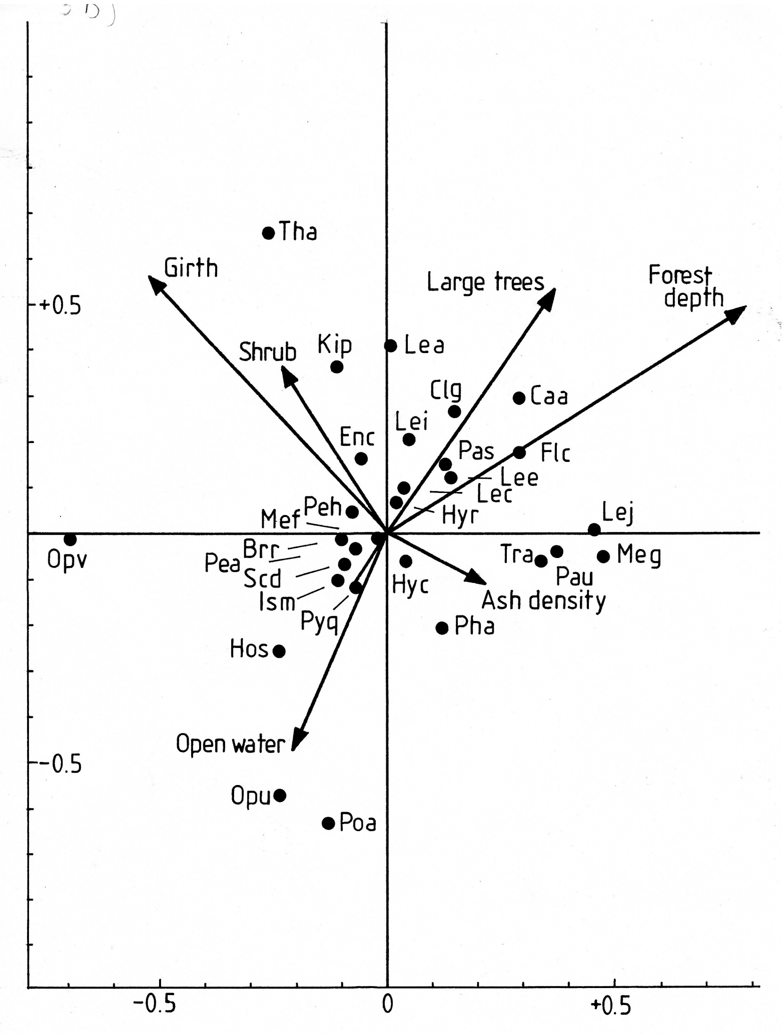

Fig. 4. Canonical community ordinations for a reduced data set: Ordination of the 28 most abundant taxa/ taxon groups in terms of cover: Brr *Brachythecium rutabulum*; Caa *Catinaria atropurpurea*; Clg *Cliostomum griffithii*; Enc *Enterographa crassa*; Flc *Flavoparmelia caperata*; Hos *Homalothecium sericeum*; Hyc *Hypnum cupressiforme*; Hyr *Hypnum resupinatum*; Ism *Isothecium myosuroides/alopecuroides*; Kip *Kindbergia praelonga*; Lea *Lecanactis abietina*; Lec *Lecanora chlarotera*; Lee *Lecanora expallens*; Lei *Lepraria incana* agg.; Lej *Lecanora* cf *jamesii*; Mef *Metzgeria furcata*; Meg *Melanelixia fuliginosa* subsp. *glabratula*; Opv *Opegrapha varia*; Opu *Opegrapha vulgata*; Pas *Parmelia saxatilis*; Pea *Pertusaria albescens + P. amara*; Peh *Pertusaria hymenea*; Poa *Porina aenea*; Pyq *Pyrrhospora quernea*; Scd *Schismatomma decolorans*; Tha *Thamnobryum alopecurum*; Tra *Trentepohlia abietina*.

Table 6. Means and ranges for ash bark composition

Determinant	*Mean*	*Range*
Tree girth cm	214	4-473
pH	5.3*	3.2-7.3
Conductivity µS cm^{-1}	943	477-3930
Ca % dry wt.	2.55	0.82-4.51
P % dry wt.	0.021	0.011-0.057
Soluble tannins E_{450}	1.87	0.5-6.5

* Not transformed to linear scale

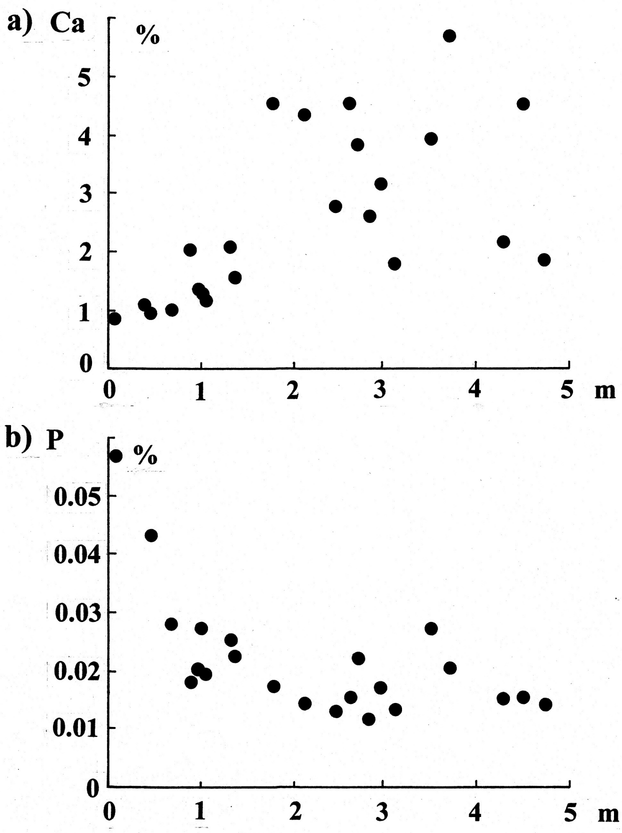

Fig. 5. Concentration as % dry weight of a) calcium and b) phosphorus in samples of bark from 24 of the ash trees in relation to girth.

DISCUSSION

For investigations of species diversity, species richness is often used although diversity indices such as Shannon and Simpson may be of value where comparisons are to be made between different forests or stands. They are capable of providing a useful summary of species composition and abundance (Hoffmann, 1971; Rasmussen, 1975) and may be used as a yardstick by which other studies can be compared. Li *et al.* (2007) for example, found a significant difference in diversity indices between the epiphytic lichens of primary and secondary forest in China. The Shannon and Simpson indices computed for this present study indicated there was little to chose between them and species richness so they provided no advantage in this respect.

The strong correlation between tree girth, as a proxy for age, and cryptogam diversity is well known (Selva 1994; Holien, 1998; Hedenås *et al.*, 2003) but the environmental interpretation is complex. Ash bark surface area increases approximately linearly with time while it remains smooth, but starts to rise exponentially as the surface becomes rough as is also the case of oak. Finally it attains a quasi- equilibrium when the trees stop growing and the surface is gradually renewed following exfoliation (cf. Pentecost, 2010). Consequently there is no ‘ideal’ sampling technique for trees such as ash. Sampling the entire bole to a fixed height has the advantage of inclusivity since aspect and height above ground, both of which influence cryptogam distribution are removed as potential variables, with the disadvantage that the sampling area is constantly changing. Species-area relationships may then obscure environmental effects (Moe & Botnen, 1997; Gotelli & Colwell, 2010). Random quadrat sampling cannot eliminate this problem owing to the variation of bark roughness with age plus the positional problems noted above. The complex relationship between bark surface area and age also make the construction of epiphyte species-area relationships for trees problematic, but multivariate methods such as CCA appear to be sufficiently robust to allow some ecological insights to be made (Palmer, 1993).

Bark-related environmental variables that are known to correlate with age include porosity, affecting water-relations (Barkman, 1958; Harris, 1972); rugosity influencing light, humidity and water-relations (Ranius *et al.*, 2008); and bark chemistry. Barkman (1958), Bates & Brown (1981) and Bates (1992) found similar bark Ca, phosphorus and pH levels for ash trees in other parts of Europe but relationships with girth were not investigated, although Gauslaa (1985) found that bark Ca + Mg was positively correlated with age. The significant correlations for both bark calcium and phosphorus with ash girth suggest that these could influence species distributions owing to their important physiological functions. Phosphorus is a major plant nutrient whose biological availability is often linked to calcium concentration due to the formation of highly insoluble calcium phosphates. In the trees investigated here, the inverse relationship between these elements suggests an age-related trend from bark eutrophy to oligotrophy. However this ignores the possibility of nutrient storage and turnover among the associated epiphytes where litter and dust may collect within the bryophyte cushions and lichen thalli. Accumulation of allochthonous material may mitigate against the effects bark ageing and nutrient depletion. Ash bark pH was found to be highly variable and Gauslaa (1985) suggested that this phenomenon, detectable even between adjacent trees, may in part be genetic. Bates (1992) found a significant positive correlation between bark calcium and pH in oak, but this was not the case with ash. In addition, Barkman (1958) suggested that bark tannins influence pH and also increase in concentration with tree age but no evidence for this was obtained, in agreement with Gauslaa (1985).

Another factor leading to a positive association of diversity with girth is the increasing amount of time available for propagules to become established. As bark ages, the probability of additional taxa colonising is increased although at the same time, available space declines and competition becomes more significant. This is offset to a degree by the ability of some taxa to overgrow others and the development of microhabitats characterised by seepage and dry bark that tend to attract a specialist flora. Despite the general increase of cryptogam cover with increasing girth, large areas of bare bark were sometimes observed on the oldest trees during this study and this did not appear to result from exfoliation. Epiphyte succession has been well documented but it is clear that at least some cryptogams, once established continue to persist as the tree ages and are not replaced by others. This appears to be the case with ash, while some general trends are also apparent such as the increase in pleurocarpous bryophytes with age (cf. Stone, 1989; Mazimpaka *et al.*, 2010). Microlichen cover also increased with age although Ellis & Coppins (2006) found that microlichen frequency declined with age in Scottish stands of *Populus tremula*.

Providing trees are not growing too closely together, they expand their canopies as they grow and a significant correlation between girth and canopy width will result. This is particularly relevant to pasture woodlands where grazing helps to maintain spacing between trees. It is also apparent that species richness increases with exposure (see Table 3) and implies that the older trees tended to be more exposed to the elements (Hoffman, 1971). Management practices may be partly responsible for this, since two of the largest trees studied were isolated individuals in open woodland and were probably retained on account of their size while their progeny were prevented from competing through grazing.

The relationship between epiphyte diversity and exposure is complex and not well understood. Exposure tends to favour the development lichens over bryophytes, owing to the greater demand for wetting/drying cycles for the former and extended periods of wetting for the latter. Support for this was found by Gauslaa & Solhaug (1996) and Moe & Botnen (1997) although other work has failed to demonstrate it (e.g. Hedenås *et al.*, 2003). Open forest glades have also been shown to provide areas of higher diversity for lichens (Moning *et al.*, 2009).

Local density of ash trees was found to be negatively correlated with species richness and total cryptogam cover. This variable was included as it was hypothesised that ash, being a tree capable to harbouring a large number of epiphytes, would, through the local dispersion of propagules, become richer in species if there were other ash trees in close proximity. This was clearly not the case here - dense groves of ash did not increase species richness, although some local transfer of individual taxa was apparent within clumps. Most of the lichens showing restricted dispersal within particular ash stands belonged to sorediate species, and Hedenås *et al.* (2003) found a similar relationship in stands of *Populus* suggesting that soredia are effective in the local dispersal of some lichens.

Buckley (2011) found that isolated *Nothofagus* trees tended to have a less diverse lichen flora. This was possibly resulting from short-range dispersal of propagules although cryptogam diversity was found to respond positively to areas of mixed woodland in Maine (Cleavitt *et al.*, 2009). There was no evidence of a reduced diversity on the isolated ash trees but only two of the 75 sampled were distant from other trees.

In their study of epiphytes of open ash stands in Norway, Moe & Botnen (1997) noted that altitude (range 10-220 m) was a significant environmental variable. They argued that as altitude increased, the trees became smaller and spread further apart with less canopy cover. Altitude did not have a significant effect on the Sussex ash flora, perhaps owing to the more limited range of values (70-145 m) although tree girth was negatively correlated to it (Table 1). This might result from the fact that clay soils predominated at the lower altitudes while sandy soils, that are less favourable to ash, occurred at the highest sites. If this is the case, the effect appears to be marginal with respect to epiphyte colonisation. At this lower latitude, a small difference in altitude probably has less effect on climate that in Norway.

Proximity to open water also appears to be factor that is important to some cryptogams although the reason for this is not apparent. Correlation was negative with microlichen cover despite the fact that a few taxa were positively influenced by it. A similar observation was made by Lidén & Hilmo (2005) with the macrolichen *Platismatia norvegica*.

The amount of forest cover surrounding the trees revealed some interesting trends. The “mean depth”, an estimate of the amount of continuous woodland surrounding each site at the cardinal points, correlated with both macrolichen and microlichen cover and featured prominently in the ordination. These correlations are probably related to the fact that the larger trees tended to occur deeper within the wood and had a higher lichen cover (Table 3). Ellis & Coppins (2007) found that species richness was positively related to woodland extent in their survey of Scottish forests and the influence of forest size is worthy of further investigation.

This investigation lends support to the current management strategies for ancient pasture woodland in the UK and has relevance to the conservation of cryptogamic epiphytes in general. Current practice for ancient pasture woodland foster a diverse tree flora with open glades and retention of veteran trees. Forest fragmentation by felling is to be avoided and low-level large herbivore grazing encouraged. These activities are capable of maintaining a high biodiversity in a semi-natural woodland environment (Ferris & Humphrey, 1999; Sanderson & Wolseley, 2001). The cryptogamic epiphytes of ash are of particular importance and the conservation of veteran trees as hosts of a rich and varied epiphyte flora should be a priority. This is particularly important in view of recent concerns over the pathogen *Chalara fraxinea*, the cause of ash dieback disease that is currently spreading throughout Europe (Kowalski, 2006). At the Sussex site, the age-structure of the ash population is uneven and this will probably lead to a decline in veteran trees and significant loss of cryptogam diversity in the future, owing to limited dispersal of propagules and lack of a suitable substratum. There is also a suggestion that the maintenance of open water areas could be significant for some species. Lichens and bryophytes tend to occupy different ecological niches and some areas of high humidity and shelter need to be included. This would be best achieved by encouraging/maintaining open glades of a range of sizes to provide niches allowing both bryophyte-rich and lichen-rich assemblages to flourish.

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REFERENCES

ANDERSEN J.M., 1976 — An ignition method for the determination of total phosphorus in lake sediments. *Water research* 10: 329-331.

BATES J.W. & BROWN D.H., 1981 — Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* in a maritime area of south west England. *Vegetatio* 48: 61-70.

BATES J.W., 1992 — Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. *Journal of ecology* 80: 163-180.

BARKMAN J.J., 1958 — *Phytosociology and Ecology of Cryptogamic Epiphytes*. Assen, Van Gorcum, 628 p.

BUCKLEY H.L., 2011 — Isolation affects true-scale epiphytic lichen community structure on New Zealand mountain beech trees. *Journal of Vegetation science* 22: 1062-1071.

CLEAVITT N.L., DIBBLE A.C. & WERIER A., 2009 — Influence of tree composition upon epiphytic macrolichens and bryophytes in old forests of Acadia National Park. *The bryologist* 112: 467-487.

EATON A.D., RICE E.W. & BIRD R.B., 2010 — *Standard Methods for the Examination of Water and Wastewater.* Washinton, D.C., American Public Health Association, 1466 p.

ELLIS C.J. & COPPINS B.J., 2006 — Contrasting functional traits maintain epiphyte diversity in response to climate and succession. *Journal of biogeography* 33: 1643-1656.

ELLIS C.J. & COPPINS B.J., 2007 — Nineteenth Century woodland structure controls stand-scale epiphyte diversity in present-day Scotland. *Diversity and distributions* 13: 84-91.

ELLIS C.J., YAHR, R. & COPPINS, B.J., 2009 — Local extent of old-growth woodland modifies epiphyte response to climate change. *Journal of biogeography* 36: 302-313.

ELLYSON W.J.T. & SILLETT S.C., 2003 — Epiphyte communities in old-growth redwood forest. *The bryologist* 106: 192-211.

FERRIS R. & HUMPHREY J.W., 1999 — A review of potential biodiversity indicators for application in British forests. *Forestry* 72: 313-328.

GAUSLAA Y., 1985 — The ecology of *Lobarion pulmonariae* and *Parmelion caperatae* in *Quercus* dominated forests in south-west Norway. *The lichenologist* 17: 117-140.

GAUSLAA Y. & SOLHAUG, K.A., 1996 — Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal stands. *Functional biology* 10: 344-354.

GILBERT O.L., 2000 — *Lichens*. Harper Collins, London, 288 p.

GOTELLI N. J. & COLWELL, R.K., 2010 — Estimating species richness. *In*: Magurran A.E. & McGill B.J. (Eds), *Frontiers in measuring biodiversity*. New York, Oxford University Press, pp. 39-54.

HARRIS G.P., 1972 — The ecology of corticolous lichens II. A simulation model of productivity as a function of light intensity and water availability. *Journal of ecology* 60: 19-40.

HEDENÅS H., BOLYUKH, V.O. & JONSSON B.G., 2003 — Spatial distribution of epiphytes on *Populus tremula* in relation to dispersal mode. *Journal of vegetation science* 14: 233-242.

HILL M.O., BELL N., BRUGGEMAN-NANNENGA M.A., BRUGUES M., CANO M.J., ENROTH J., FLATBERG K.I., FRAI I.M., GALLEGO M.T., GARILLETI R., GUERRA J., HEDENÅS L., HOLYOAK D.T., HYVONEN J., IGNATOV M. S., LARA F., MAZIMPAKA V., MUNOZ J. & SÖDERSTRÖM L., 2006 — An Annotated Checklist of the Mosses of Europe and Macaronesia. *Journal of bryology* 28: 198-267.

HOFFMANN G.R., 1971 — An ecologic study of epiphytic bryophytes and lichens in *Pseudotsuga menziesii* on the Olympic Peninsula, Washington. II Diversity of the vegetation. *The bryologist* 74: 413-427.

HOLGATE P., 1967 — The angle-count method. *Biometrika* 54: 615-623.

HOLIEN H., 1998 — Lichens in spruce forest stands of different successional stages in central Norway with emphasis on diversity and old growth species. *Nova Hedwigia* 66: 283-324.

IHLEN P.G., GJERDE I. & SAETERSDAL M., 2001 — Structural indicators of richness and rarity of epiphytic lichens on *Corylus avellana* in two different forest types within a nature reserve in south-western Norway. *The lichenologist* 33: 215-229.

KOWALSKI T., 2006 — *Chalara fraxinea* sp. nov. associated with dieback of ash (*Fraxinus excelsior*) in Poland. *Forest Pathology* 36: 264-270.

LI S., LIU W., WANG L., LANG G. & LI D., 2007 — Species diversity and distribution of epiphytic lichens in the primary and secondary forests in the Ailao Mountains, Yunnan. *Shengwu Duoyangxing* 15: 445-455.

LIDÉN M. & HILMO O., 2005 — Population characters of the suboceanic lichen Platismatia norvegica in core and fringe habitats: relationships to macroclimate, substrate and proximity to streams. The bryologist 108: 506-517.

MAGURRAN A., 1988 — Ecological diversity and its Measurement. Princeton, N.J., Princeton University Press, 129 p.

MAZIMPAKA V., MEDINA N.G., LO GUIDICE R., GARILLETI R. & LARA F., 2010 — Tree age-dependent changes among epiphytic bryophyte communities in a Mediterranean environments. A case study from Sicily. Plant biosystems 144: 241-249.

MOE B. & BOTNEN A., 1997- A quantitative study of the epiphytic vegetation on pollarded trunks of Fraxinus excelsior at Havra, Osteroy, western Norway. Plant ecology 129: 157-177.

MONING C., WERTH S., DZIOCK F., BASSLER C., BRADKA T., HOTHORN T. & MULLER J., 2009 — Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest ecology and management* 258: 745-751.

MORLEY S.E. & GIBSON M., 2010 — Successional changes in epiphytic rainforest lichens: implications for the management of rainforest communities. *The lichenologist* 42: 311-321.

PALMER M.W., 1993 — Putting things in even better order: The advantages of Canonical Correspondence Analysis. *Ecology* 78: 2215-2230.

PENTECOST A. & ZHANG Z., 2006 — Response of bryophytes to exposure and water availability on some European travertines. *Journal of bryology* 28: 21-26.

PENTECOST A., 2010 — Bark surface area in English woodlands – how much is there and how much do we sample? *British lichen society bulletin* 107: 35-43.

PENTECOST A. & RICHARDSON C.B., 2011 — Niche separation and overlap in the foliose lichens *Lobaria pulmonaria* (L.) Hoffm. and *L. virens* (With.) Laundon in the Killarney oakwoods, Ireland. *Biology and environment* 111 B : 61-67.

PETTERSON R.B., BALL J.P., RENHORN K.-E., ESSEEN P.-A. & SJOBERG K., 1995 — Invertebrate communities in boreal forest canopies, as influenced by forest and lichens, with implications of passerine birds. *Biology and conservation* 74: 57-63.

PYATT D.G., HARRISON D. & FORD A.S., 1969 — Guide to site types in forests of North and Mid Wales. *Forest record* 69: 1-24.

RANIUS T., JOHANSSON P., BERG N. & NICKLASSON M., 2008 — The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. *Journal of vegetation science* 19: 653-662.

RASMUSSEN L., 1975 — The bryophyte epiphyte vegetation in the forest Slotved Skov, Northern Jutland. *Lindbergia* 3: 15-38.

ROSE F., 1976 — Lichenological indicators of age and environmental continuity I woodlands. *Systematics association special volume* 8: 279-307.

ROSE F., 1988 — Phytogeographical and ecological aspects of *Lobarion* communities in Europe. *Botanical journal of the Linnean society* 96: 69-79.

SANDERSON N. & WOLSELEY P., 2001 — Management of pasture woodlands for lichens. *In*: Fletcher A. (ed.) *Lichen Habitat Management.* [London], British Lichen Society, pp. 05/1-05/21

SELVA S.B., 1994 — Lichen diversity and stand continuity in the Northern Hardwoods and spruce-fir forests of northern New England and western New Brunswick. *The bryologist* 97: 424-429.

SMITH C.W., APTTROOT A., COPPINS B.J., FLETCHER A., GILBERT O.L., JAMES P.W. & WOLSELEY P.A., 2009 — *The Lichens of Great Britain and Ireland.* London, British Lichen Society, 1046 p.

SÖDERSTRÖM L., URMI E. & VÁŇA J., 2007 — The distribution of Hepaticae and Anthocerotae in Europe and Macaronesia – Update 1-406. *Cryptogamie, Bryologie* 28: 299-350.

STACE C., 1991 — *New Flora of the British Isles.* Cambridge, New York, Cambridge University Press. 1226 p.

STONE D.F., 1989 — Epiphyte succession on *Quercus garryana* branches in the Williamette Valley of western Oregon. *The bryologist* 92: 81-94.

TER BRAAK C.J.F., 1987 — The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-77.

TER BRAAK C.J.F. & SMILAUER P., 1998 — *Canoco reference manual and software for Canonical Community Ordination (version 4).* Centre for Biometry, Wageningen. 351 p.

VAN HERK C.M., 2001 — Bark pH and susceptibility to toxic air pollutants as independent causes in epiphytic lichen communities in space and time. *The lichenologist* 33: 419-441.

WALSER J-C., ZOLLER S., BÜCHLER U. & SHEIDEGGER C., 2002 — Species-specific detection of *Lobaria pulmonaria* (lichenized ascomycete) diaspores in litter samples trapped in snow. *Molecular ecology* 10: 2129-2138.

WARDLE P., 1961 — Biological Flora of the British Isles. *Fraxinus excelsior* L. *Journal of ecology* 49: 739-751.

Appendix to Table 5

Cover and (frequency) estimates of remaining 103 epiphyte species: *Phlyctis argena*, 1.1 (45); *Cliostomum griffithii*, 1.1 (35); *Schismatomma decolorans*, 1.0 (17); *Opegrapha varia*, 1.0 (6.7); *Catinaria atropurpurea*, 0.85 (9.3); *Homalothecium sericeum*, 0.83 (13); *Pertusaria albescens*, 0.79 (3.9); *Lecanactis abietina*, 0.77 (16); *Melanelixia fuliginosa* subsp. *glabratula*, 0.75 (49); *Thamnobryum alopecurum*, 0.68 (6.7); *Flavoparmelia caperata*, 0.6 (41); *Porina aenea*, 0.34 (5.3); *Pertusaria amara*, 0.34 (27); *Pyrrhospora quernea*, 0.33 (21); *Opegrapha vulgata*, 0.29 (17); *Lecanora chlarotera*, 0.28 (35); *Pertusaria hymenea*, 0.27 (28); *Parmelia saxatilis*, 0.25 (20); *Thelotrema lepadinum*, 0.25 (9.3); *Haematomma ochroleucum* var. *porphyrium*, 0.23 (2.7); *Pertusaria pertusa*, 0.22 (17); *Opegrapha rufescens*, 0.20 (6.7); *Neckera complanata*, 0.20 (1.3); *Ochrolechia androgyna*, 0.20 (13); *Parmotrema perlata*, 0.20 (21); *Pertusaria coccodes*, 0.19 (12); *Orthotrichum affine*, 0.18, (32); *Arthonia spadicea*, 0.16 (15); *Frullania dilatata*, 0.15 (16); *Hypotrachyna revoluta*, 0.14 (24); *Lecidella elaeochroma*, 0.11 (12); *Bacidia phacodes*, 0.11 (8); *Caloplaca ulcerosa*, 0.11 (5.3); *Microlejeunea ulicina*, 0.09 (15); *Hypogymnia physodes*, 0.09 (11); *Punctelia subrudecta*, 0.08 (15); *Mnium hornum*, 0.08 (8); *Cladonia coniocraea*, 0.07 (28); *Arthonia radiata*, 0.07 (15); *Chrysothrix candelaris*, 0.07 (11); *Homalia trichomanoides*, 0.05 (2.7); *Lecanora sublivescens*, 0.05 (1.3); *Mycoblastus fucatus*, 0.05 (9.3); *Ramalina farinacea*, 0.05 (33); *Caloplaca obscurella*, 0.04 (2.7); *Ochrolechia subviridis*, 0.04 (1.3); *Bacidia incompta*, 0.04 (1.3); *Opegrapha herbarum*, 0.03 (9.3); *Rinodina roboris*, 0.03 (4); *Calicium viride*, 0.03 (2.7); *Metzgeria fruticulosa*, 0.03 (1.3); *Lecania cyrtellina*, 0.03 (1.3); *Evernia prunastri*, 0.03 (13); *Chaenotheca ferruginea*, 0.03 (5.3); *Candelariella reflexa*, 0.03 (13); *Bacidia laurocerasi*, 0.03 (1.3); *Bacidia delicata*, 0.03 (1.3); *Arthonia* sp., 0.03 (1.3); *Pertusaria hemisphaerica*, 0.02 (5.3); *Bryum capillare*, 0.02 (8); *Gyalecta truncigena*, 0.02 (4); *Syntrichia laevipila*, 0.01 (2.7); *Radula complanata*, 0.01 (1.3); *Lecanora* cf. *compallens*, 0.01 (1.3); *Plagiomnium affine*, 0.01 (5.3); *Ochrolechia turneri*, 0.01 (2.7); *Graphis scripta*, 0.01 (5.3); *Amandinea punctata*, 0.01 (4); *Pertusaria leioplaca*, 0.1 (1.3); *Zygodon viridissimus*, 0.1 (2.7); *Xanthoria parietina*, 0.01 (5.3); *Rinodina* sp. 0.1 (2.7); *Lophocolea cuspidata*, 0.01 (2.7); *Dimerella pineti*, 0.01 (4); *Ulota crispa*, 0.05 (4); *Physcia adscendens*, 0.05 (4); *Opegrapha ochrocheila*, 0.05 (2.7); *Normandina pulchella*, 0.05 (4); *Graphis elegans*, 0.05 (2.7); *Cladonia digitata*, 0.05 (2.7); *Thuidium tamariscinum*, 0.02 (1.3); *Pyrenula chlorospila*, 0.02 (2.7); *Plagiomnium cuspidatum*, 0.02 (1.3); *Fuscidea lightfootii*, 0.02 (1.3); *Flavoparmelia soredians*, 0.02 (1.3); *Dicranum scoparium*, 0.02 (1.3); *Cyphelium sessile*, 0.02 (1.3); *Catillaria nigroclavata*, 0.02 (1.3); *Atrichum undulatum*, 0.02 (1.3); *Punctelia reddenda*, 0.01 (1.3); *Phaeographis dendritica*, 0.01 (1.3); *Parmotrema reticulata* 0.01 (1.3); *Pachyphiale carneola*, 0.01 (1.3); *Opegrapha atra*, 0.01 (1.3); *Micarea denigrata*, 0.01 (1.3); *Lecania naegelii*, 0.01 (1.30); *Dryopteris filix-mas*, 0.01 (1.3); *Diploicia canescens*, 0.01 (1.3); *Ceratodon purpureus*, 0.01 (1.3); *Caloplaca flavovirescens*, 0.01 (1.3); *C. citrina*, 0.01 (1.3); *Buellia griseovirens* 0.01 (1.3).