



Original research article

Diversity and distribution of epiphytic bryophytes on Bramley's Seedling trees in East of England apple orchards



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HIGHLIGHTS

- The epiphytic bryophyte flora of four UK bramley orchards was surveyed.
- Tree size and shape account for around 10% of the variation in the bryophyte flora.
- Orchard management can impact diversity and distribution of epiphytic bryophytes.

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ABSTRACT

Epiphytic bryophytes on apple trees were investigated in relation to a selection of tree characteristics. Management of orchard trees for fruit production affects the habitats available for colonisation and growth of epiphytes on trunks and branches. Bryophytes recorded on Bramley's Seedling apple trees in orchards in Hertfordshire and Cambridgeshire showed a high level of similarity in species composition between the orchards. The similarity between orchards was, however, much reduced when relative species cover on the trees was taken into account. Twenty three species were recorded on the 71 trees sampled for detailed investigation. Tree structure, as determined by management, explained about 10% of the observed variation in bryophyte cover. Within that, trunk girth and distance to nearest neighbouring orchard trees were the most important factors. This information is of value to orchard managers aiming to become more proactive in managing their habitats for the benefit of biodiversity.

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1. Introduction

Epiphytic lichens and bryophytes are often studied as useful indicators of habitat quality, both in relation to air quality (Davies et al., 2007) and, for example, in considering woodland and forest planting (Hazell et al., 1998). This was the case especially in relation to industrial pollution and subsequent improvements in air quality following controls on pollutant emissions. In the south and east of England, for example, studies by Bates et al. (1997, 2004) focussed on bryophytes growing on standard trees along roadsides and at woodland edges. Smith (1982) reviewed the relationships between epiphytic bryophytes and some tree characteristics, including structure and bark chemistry. Very little was published on orchards, however, until Stevenson and Rowntree (2009) suggested that the planting and management of orchard trees can provide a readily sampled habitat for comparing single species and single variety studies of diversity and abundance of epiphytic bryophytes. Orchards, groups of fruit trees planted for food production, have, and continue to be, an economically important

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Table 1
Location and features of orchards.

Orchard	Location	Approx planting date	Tree structure
Oaklands College	St Albans, Hertfordshire	1980	Young half standard
St Elizabeth's	Much Hadham, Hertfordshire	1930	Bush/half-standard
Tewin	Tewin, Hertfordshire	1930	Bush
Aldreth 70	Haddenham, Cambridgeshire	1930	Half standard
Aldreth 100	Haddenham, Cambridgeshire	1900	Half standard

part of the British landscape. However, in recent times fruit has been sourced from elsewhere and many orchards have fallen into disrepair or been removed altogether (Robertson and Wedge, 2008). It is estimated that there has been a 63% reduction in the area of England given over to orchards since the 1950s (NE, 2008). Although there has been a recent small increase in commercial orchards (Defra, 2013) overall, loss of orchard habitat is still considerable and on-going (Burrough and Robertson, 2008; Burrough et al., 2010). Traditional Orchards are identified as a priority habitat in the UK Post 2010 Biodiversity Framework due to the high level of biodiversity they can support. Fruit trees are the main feature of orchard habitats and these have been found to host a high diversity of epiphytes, particularly bryophytes and lichens (Lush et al., 2009; Robertson et al., 2012; Stevenson and Rowntree, 2009).

This study aimed to record epiphytic bryophyte diversity in a selection of apple orchards in the East of England and to identify aspects of the management of the habitats that were important in contributing to epiphytic bryophyte diversity and abundance. By identifying variables which are under the control of orchard owners is hoped that the insights can be used to aid orchard owners in becoming more proactive in managing their habitats for the benefit of biodiversity.

2. Methods

2.1. Site selection and descriptions

Suitable survey sites were identified through contacts with local individuals, the Hertfordshire Biological Records Centre and the Hertfordshire Orchard Initiative.

Four sites, three in Hertfordshire and one in Cambridgeshire (consisting of two different aged orchards), were selected for surveys (Table 1) between 2009 and 2011 and a total of 71 trees were sampled. The surveys were restricted to a single variety, Bramley's Seedling, the most common single variety of cooking apple (*Malus domestica*) grown in the UK (Defra, 2013). The orchards differed in age with the youngest having been planted in 1980 and, apart from Aldreth 100, contained mixed varieties. The oldest orchard (Aldreth 100) was planted over 100 years ago but the exact date of planting was not known. Species accumulation curves showed that 10 trees of the same variety within an orchard were sufficient to represent the orchard and a random number generator was used to select these. The position of each tree surveyed was recorded using GPS.

Bryophytes were identified following Atherton et al. (2010) and Smith (2004). No subspecies were recorded and it was not possible to distinguish between the frequently infertile *Ulota crispa* and *Ulota bruchii* in the field.

2.2. Survey methods

All bryophytes on the trunks and branches of the trees were recorded up to a height of around 2 m. Any bryophytes growing higher than this were not identified but were included in estimates of total bryophyte cover.

To record bryophyte cover a visual estimate of the area covered by each species was made using a 4 cm² grid as a reference. Area was recorded as multiples of this reference area. Although it is generally acknowledged that visual estimates are not the best method for measuring plant cover the irregular nature of the epiphytic flora and the structure of the trees themselves made other methods, such as the pin-point or point-intercept method (Kershaw and Looney, 1985) difficult to implement.

Five tree characteristics were measured: tree height, estimated using an abney level; trunk height; trunk girth; canopy area calculated using the equation for the area of an ellipse; and distance to nearest orchard tree. An Extech pH100 flat headed pH meter (EIC, 2010) was used to record bark pH. Three separate areas of bark, on primary branches free of epiphytes, were dampened with a 1M solution of potassium chloride and the pH was recorded when the reading had stabilised for 10 s.

2.3. Data transformations and analysis

Bark pH values for each tree were calculated from H⁺ ion concentration using the equation $H^+ = 10^{-pH}$, using the mean value from the three readings. This value was then converted back to pH units ($pH = -\log_{10}(H^+)$).

One-way analysis of variance (ANOVA) and post-hoc test Tukey's pairwise comparisons were undertaken using the free data analysis package Paleontological Statistics (PAST) version 2.14 (Hammer, 1999). Sørensen Similarity indices, Bray-Curtis similarity indices, Analysis of similarity (ANOSIM), Similarity percentages (SIMPER) and Detrended Correspondence Analysis (DCA) were carried out using CAP3 (Seaby and Henderson, 2007), Pearson correlations with scattergraphs and Canonical correspondence analysis (CCA) were carried out using ECON (PISCES, 2007).

Table 2

Total bryophyte species, mean number of bryophyte species recorded per tree and mean bryophyte cover per tree recorded during each survey.

	Oaklands College	St Elizabeth's	Tewin	Aldreth 70	Aldreth 100
Total species recorded	14	10	18	19	16
Mean number of species per tree	6.2	3.4	8.5	9	6.4
Mean bryophyte cover per tree (cm ²)	286	90	2189	2754	1069

Table 3

Bryophyte species recorded during each survey expressed as % of trees surveyed. *N* = 10 except in Oaklands (*N* = 20), St Elizabeth's (*N* = 16) and Tewin (*N* = 15). T = Tewin, O = Oaklands College, StE = St Elizabeth's, A70 = Aldreth Road (70 year old trees), A100 = Aldreth Road (100+ year old trees).

	Oaklands College	St Elizabeth's	Tewin	Aldreth 70	Aldreth 100
Pleurocarps					
<i>Amblystegium serpens</i>	15	25	60	80	20
<i>Brachythecium rutabulum</i>	85	44	53	80	60
<i>Brachythecium velutinum</i>	55	6	80	90	40
<i>Cryphaea heteromalla</i>	–	–	7	–	–
<i>Homalothecium sericeum</i>	–	–	33	90	20
<i>Hypnum cupressiforme</i>	90	75	100	100	100
<i>Hypnum resupinatum</i>	–	–	–	20	10
<i>Leucodon sciuroides</i>	–	–	–	10	–
<i>Rhynchostegium confertum</i>	20	–	87	30	60
Acrocarps					
<i>Bryum capillare</i>	60	44	87	80	60
<i>Campylopus introflexus</i>	5	–	–	10	–
<i>Dicranoweisia cirrata</i>	35	6	33	50	30
<i>Grimmia pulvinata</i>	10	–	20	–	–
<i>Orthotrichum affine</i>	90	38	73	70	40
<i>Orthotrichum diaphanum</i>	60	63	73	40	60
<i>Orthotrichum lyellii</i>	20	–	13	10	–
<i>Syntrichia intermedia</i>	–	–	–	10	20
<i>Syntrichia papillosa</i>	–	–	13	–	40
<i>Syntrichia virescens</i>	–	31	–	70	60
<i>Ulota crispa/bruchii</i>	25	–	27	–	–
<i>Zygodon viridissimus</i>	45	6	53	30	10
Liverworts					
<i>Frullania dilatata</i>	–	–	20	20	–
<i>Metzgeria furcata</i>	–	–	20	10	10

For Detrended Correspondence Analysis and Canonical Correspondence Analysis, bryophyte cover data were transformed using the equation $\log_{10}(x + 1)$, where *x* is the cover value in cm². This reduced the influence of species with very high levels of cover compared to other species (Henderson and Seaby, 2008).

3. Results

3.1. Bryophyte diversity and cover

The orchard trees represented a variable habitat for epiphytic bryophytes, with the number of species recorded varying between 10 and 21. The mean number of species recorded per tree were similarly variable and loosely linked to total species for each orchard (see Table 2). The orchards with fewer species overall and fewer mean species per tree also had lower mean bryophyte cover.

A total of 23 species were recorded, 21 mosses and 2 liverworts (see Table 3). None of these were unexpected for the habitat or area. *Hypnum cupressiforme* was recorded most frequently. *Bryum capillare*, *Brachythecium rutabulum*, *Orthotrichum affine* and *O. diaphanum* were also relatively frequent. Two species, *Cryphaea heteromalla* and *Leucodon sciuroides*, were recorded only once across all surveys.

There was a high degree of species overlap between the orchards. Sørensen similarity index, comparing species presence/absence between orchards, returned results of between 64% and 86% similarity, perhaps not surprising given the superficial similarity between the habitats and the single apple variety sampled. However, species overlap was much lower when frequency data (how often a species was recorded in an orchard) was taken into account. The Bray-Curtis method (Greig-Smith, 1983), returned results of between 25% and 38%.

The cover of individual bryophytes across orchards was also extremely variable. *Hypnum cupressiforme* again dominated the assemblages, accounting for almost 50% of the total bryophyte cover across all orchards. The two next most abundant species *Brachythecium rutabulum* and *Bryum capillare* accounted for far less of the total bryophyte cover, 16% and 10%

Table 4

Mean and range of bark pH recorded at each orchard. $N = 10$ at Aldreth (70) and Aldreth (100+), $N = 20$ at Oaklands, $N = 16$ at St Elizabeth's and $N = 15$ at Tewin.

	Mean pH	Range
Oaklands	5.19	4.57–6.05
St Elizabeth's	5.07	4.66–5.84
Tewin	5.06	4.54–6.15
Aldreth (70)	4.78	4.30–5.73
Aldreth (100)	5.23	4.88–6.97

respectively. In contrast the 15 less abundant species accounted for just under 10% of the total bryophyte cover between them. Across the orchards total bryophyte cover was significantly correlated with number of individual bryophyte species ($R^2 = 0.66$, $P < 0.001$).

3.2. Correlations between tree characteristics and bryophytes

Tree structural characteristics reflect their management in the orchards. Wider spacing of orchard trees would indicate an intention to allow the trees to grow larger, with large canopies, and this is reflected in the data. The strongest positive correlations ($p < 0.01$) were found between canopy area (mean = 49 m²) and trunk girth (mean = 1.3 m), tree height (mean = 5.6 m) and distance to the nearest orchard tree (mean = 6.5 m). Taller trees (up to 8.7 m), with wide canopies (up to 120 m²) generally had shorter trunks (down to 0.55 m); weaker negative correlations were found between trunk height (mean = 1 m) and the other tree characteristics.

Each tree characteristic was analysed using a one-way analysis of variance (ANOVA) with orchard as the between-groups variable. The differences between orchards were found to be significant for each tree characteristic, $P < 0.01$ in all cases. Tukey's pairwise comparison was carried out as a post-hoc test to identify any significant differences between orchards. Based on tree characteristics St Elizabeth's and Aldreth 100 were the most similar orchards, differing significantly only in trunk girth. Oaklands was significantly different from both Tewin and Aldreth 70 in all of the measured variables.

Significant positive correlations ($P < 0.01$) were found between the total cover and the number of bryophytes with the tree management-related variables tree height, trunk girth and canopy area. The distance to nearest orchard tree also showed a significant correlation with total bryophyte cover ($P < 0.01$) but not with the number of individual bryophyte species. There was less than half a pH unit difference in the mean values for bark pH across the orchards (Table 4) and there was no correlation with the number of species or cover.

3.3. Multivariate analysis

The cover of individual bryophytes on a tree resembled the assemblages on trees within the same orchard more closely than assemblages on trees from other orchards (Fig. 1). This is confirmed by an ANOSIM of orchard groupings based on the cover of individual bryophyte species showing the groupings were significant ($r = 0.458$, $P = 0.001$ for all pairs of groups).

The DCA plot (Fig. 1) and the results of the ANOSIM strongly suggest that the particular assemblage and cover distribution of bryophytes in each orchard is unique to that orchard. An ANOSIM where the trees were grouped by age rather than location found that these groupings were not significant ($r = 0.071$, $P = 0.134$) thus tree age was not an important factor in explaining the variation in the bryophyte flora across these orchards.

The results of the SIMPER analysis showed that *Hypnum cupressiforme* was the most important species in contributing to the similarity within orchard groupings. *H. cupressiforme*, contributed to between 29% and 54% of the similarity within an orchard and this species was found in large quantities on most of the trees surveyed.

Within the DCA plot (Fig. 1) the species with more widespread distributions are found in the centre of the plot. *Hypnum cupressiforme*, *Bryum capillare*, *Orthotrichum affine* and *Brachythecium velutinum* were all recorded in every orchard on a large proportion of the surveyed trees and, as a result, show no association with any particular grouping of trees. Other species appear to show a preference for certain groupings of trees within the DCA plot. Some, such as *Cryphaea heteromalla* were recorded only once and so there is insufficient data to draw conclusions about the preferences of these species. There is some indication that other species may be associated with the type of cover recorded in particular orchards.

Further analysis was carried out in order to identify the tree variables which most strongly influenced the bryophyte distributions. A CCA (Fig. 2) was carried out using the data on individual bryophyte species cover on the Bramley trees, alongside the data on tree characteristics which were input as environmental variables: tree height, trunk height, trunk girth, canopy area and nearest orchard tree. An initial analysis found a high level of multicollinearity between the environmental variables. The regression of canopy area against bryophyte cover had a high R^2 score ($R^2 = 0.819$) and a high Variance Inflation Factor score (VIF = 5.549). Since canopy area was significantly correlated with a number of other characteristics this variable was removed from the analysis.

The CCA analysis (Fig. 2) showed that 10.3% of the variation in individual bryophyte cover recorded in the orchards could be explained by the recorded tree characteristics which are related to orchard management. Axis one was positively

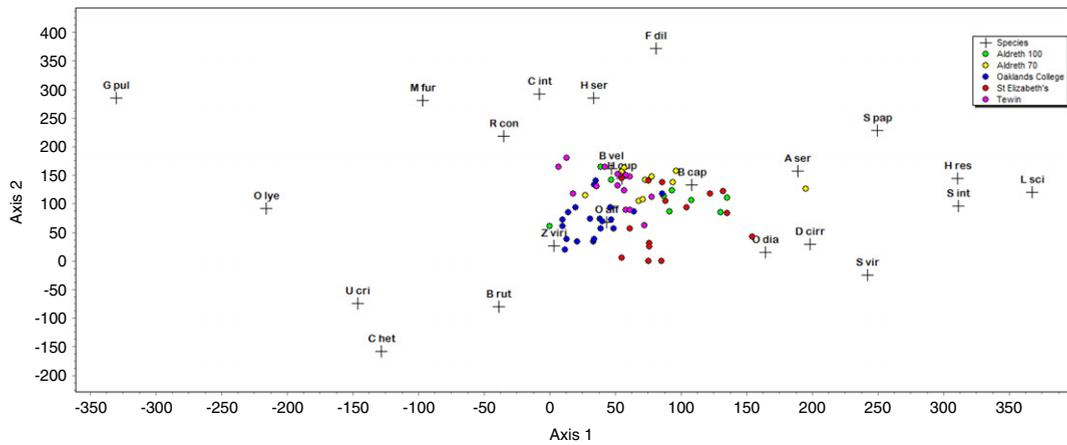


Fig. 1. Detrended correspondence analysis plot of Bramley trees and bryophyte species based on bryophyte cover. Trees, denoted by squares, which are more similar in terms of epiphytic bryophyte cover composition are positioned closer together on the plot. Colour indicates the orchard of origin of each tree. Bryophyte species are denoted with a cross. A ser = *Amblystegium serpens*, B cap = *Bryum capillare*, B rut = *Brachythecium rutabulum*, B vel = *Brachythecium velutinum*, C het = *Cryphaea heteromalla*, C int = *Campylopus introflexus*, D cirr = *Dicranoweisia cirrata*, F dil = *Frullania dilatata*, G pul = *Grimmia pulvinata*, H cup = *Hypnum cupressiforme*, H res = *Hypnum resupinatum*, H ser = *Homalothecium sericeum*, L sci = *Leucodon sciurioides*, M fur = *Metzgeria furcata*, O aff = *Orthotrichum affine*, O dia = *Orthotrichum diaphanum*, O lye = *Orthotrichum lyellii*, S int = *Syntrichia intermedia*, S pap = *Syntrichia papillosa*, S vir = *Syntrichia virescens*, U cri = *Ulota crispa/bruchii*, Z viri = *Zygodon viridissimus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

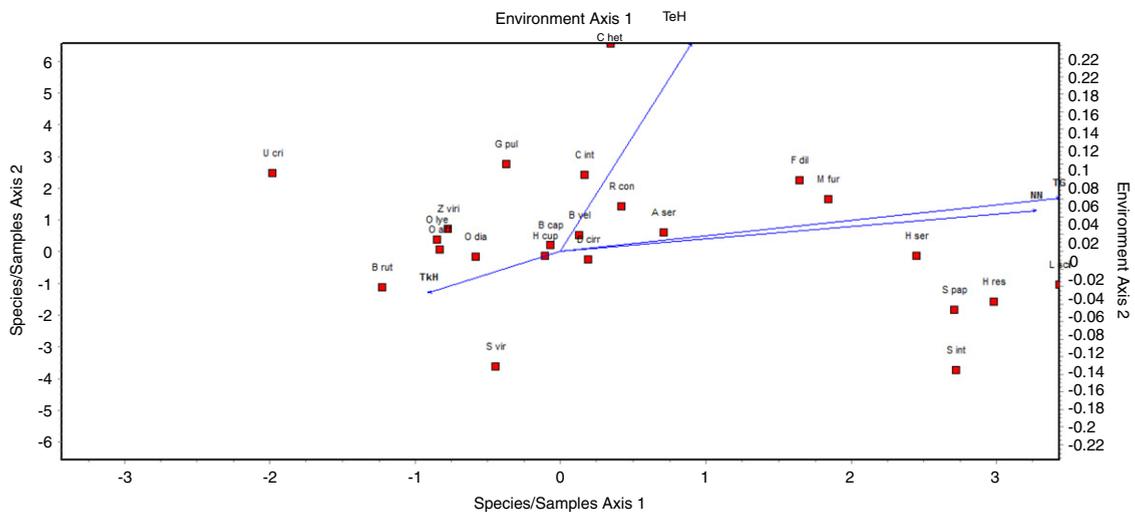


Fig. 2. Canonical correspondence analysis showing axis one and two of the species ordination. Environmental variables; TKH = Trunk Height, TeH = Tree Height, TG = Trunk Girth, NN = Nearest Orchard Tree. A ser = *Amblystegium serpens*, B cap = *Bryum capillare*, B rut = *Brachythecium rutabulum*, B vel = *Brachythecium velutinum*, C het = *Cryphaea heteromalla*, C int = *Campylopus introflexus*, D cirr = *Dicranoweisia cirrata*, F dil = *Frullania dilatata*, G pul = *Grimmia pulvinata*, H cup = *Hypnum cupressiforme*, H res = *Hypnum resupinatum*, H ser = *Homalothecium sericeum*, L sci = *Leucodon sciurioides*, M fur = *Metzgeria furcata*, O aff = *Orthotrichum affine*, O dia = *Orthotrichum diaphanum*, O lye = *Orthotrichum lyellii*, S int = *Syntrichia intermedia*, S pap = *Syntrichia papillosa*, S vir = *Syntrichia virescens*, U cri = *Ulota crispa/bruchii*, Z viri = *Zygodon viridissimus*.

correlated ($P < 0.05$) with both trunk girth ($R^2 = 0.299$) and nearest orchard tree ($R^2 = 0.285$) and suggests a gradient from trees with thinner trunks planted closer together to trees with thicker trunks planted further apart. Axis two was positively correlated ($P < 0.01$) with tree height ($R^2 = 0.237$), suggesting a gradient from short to tall trees. Trunk height is negatively correlated with the third axis, although this is a weaker correlation ($R^2 = -0.181$).

The addition of pH to the analysis was found to have very little effect on the overall ordination, with the eigenvalues for axis one and two being unchanged (0.1017 and 0.0675 respectively), and did not change the amount of variance explained by these axes.

The position of individual bryophyte species within the ordination suggests some ecological preferences. The cover of species recorded on many trees, such as *Hypnum cupressiforme* and *Bryum capillare*, are found in the centre of the ordination indicating little preference for particular tree structures. Some species, *Homalothecium sericeum*, *Hypnum resupinatum*, *Syntrichia papillosa*, are grouped towards the right of the ordination, suggesting a preference for trees with thicker trunks

planted further apart, whereas others, like *Brachythecium rutabulum* show a preference for trees with thinner trunks planted closer together.

4. Discussion

4.1. Richness of bryophyte flora

Orchards can support a relatively high number of epiphytic bryophytes. Here, 23 species of bryophyte were recorded across four orchards, with individual orchards hosting between 10 and 19 species. This is broadly in line with some other reported surveys in established orchards e.g. 8–24 per orchard (total of 33 species) in Herefordshire (Robertson et al., 2012). Lush et al. (2009) surveyed six orchards across England (one each in Cambridgeshire, Gloucestershire and Kent and three in Devon). They recorded a total of 50 species of bryophyte with a maximum of 42 species in one Cambridgeshire orchard. These surveys were not restricted to a single variety and involved free searching through the orchards.

A study of epiphytes in the south of England, which attempted to record all epiphytic bryophytes in selected 2 × 2 m squares within a transect across the country, recorded 135 species (Bates et al., 1997). The 23 species recorded here represent 17% of the species recorded by Bates et al. (1997); a relatively high proportion for a much smaller area.

Orchard trees are managed in such a way as to keep the main branches accessible for harvesting, and thus their bryophyte flora is also accessible and can be easily studied. However, this means that comparison with other epiphyte studies is difficult as most epiphyte studies have only assessed the trunks of trees. For example Davies et al. (2007) found only 14 species of bryophyte growing on oak trees in London, despite recording the epiphytic flora of 334 trees. Similarly, Bates's study of the epiphytes of oak and ash trees in western Scotland was restricted to trunk quadrats and only recorded 16 bryophyte species across 207 trees (Bates, 1992). More species may have been found had access to the canopy been possible.

The mean number of bryophyte species per tree can be a more useful indication of the habitat as a whole. The overall mean number of bryophytes per tree was 6.7. However this varied by orchard. This puts apple trees amongst the better phorophytes according to a survey of epiphytes in the south of England, where the four top ranking phorophytes (*Fraxinus excelsior*, *Sambucus nigra*, *Salix* spp and *Quercus* spp) accounted for more than half of the records made. The mean number of epiphytic bryophytes found on these species was between 4, for *Quercus* spp, and approximately 8 for *Fraxinus excelsior* (Bates et al., 2004).

4.2. Species composition

All species recorded are considered native to the UK, apart from *Campylopus introflexus* (Hill et al., 2007) which was first recorded in the UK in 1941 and is now found widely throughout the country (Atherton et al., 2010). None of the species were found outside of their expected range within the UK and, although *Syntrichia virescens* was designated as “nationally scarce” in the UK by the Joint Nature Conservation Committee (Robertson et al., 2012), who noted that this species may be under recorded due to confusion with the morphologically similar *Syntrichia intermedia*. Lush et al. (2009) found only locally rare bryophytes in their study of six orchards. This was in contrast to a number of nationally scarce species recorded in other groups of organisms. Stevenson and Rowntree (2008) noted that orchards have provided a number of new county records and occasional bryophyte rarities have been recorded for example the discovery of *Antitrichia curtispendula* on a Bramley's Seedling in Cambridgeshire (Hodgetts et al., 2006).

4.3. Influence of bark pH and tree age

Bark pH was not found to be an important factor in explaining the recorded distribution of epiphytic bryophytes, showing no correlation with total bryophyte cover nor number of bryophyte species and having little effect on the results of the CCA. This is in contrast to numerous reports of substrate pH influencing epiphytic bryophyte distributions (e.g. Barkman, 1958; Bates, 1992) and the influence of pH on the establishment and growth of bryophytes has been shown under laboratory conditions (Lobel and Rydin, 2010). In this study, pH was found to be variable both within and across orchards (Table 4). The pH was recorded from areas of the bark which did not have any bryophyte cover and may represent less suitable microhabitats for bryophyte establishment.

Tree age is often thought to be an important factor in influencing the distribution of epiphytic bryophytes. However, this was not found to be the case here where grouping of trees by age was not found to be significant. Older trees represent a longer timescale in which colonisation and growth can occur, as well as providing a larger area for colonisation (Király and Odor, 2010). In orchards, however, it was not uncommon for epiphytes to be removed from trees, for aesthetic or tree health reasons, through either trunk scraping or tar-washing (Stevenson and Rowntree, 2009) Such practices are no longer common but it does mean that the age of the tree and the length of time for which the bark has been available for colonisation may not necessarily be the same.

Atmospheric pollution has long been known to affect both bark chemistry and the growth and distribution of epiphytes. Evidence suggests that nitrogen based pollutants, oxides of nitrogen (NO₂ and NO) as well as ammonia, are detrimental to lichens and bryophytes and so can influence their distributions (Davies et al., 2007; Larsen et al., 2007). Historically high

levels of atmospheric pollutants have meant that epiphytic species have not been able to survive. Bark has been shown to become more acidic in the presence of pollutants and this, again, makes the habitat less suitable for many bryophyte species. Larsen et al. (2007) studied the epiphytic flora (lichens and bryophytes) of oak trees in London in the context of air pollution and bark pH. In their study, four species of bryophyte and 64 species of lichen were recorded, 19 of which (including two bryophytes) were correlated with nitrogen oxides, suggesting that they had been affected by London's transport emissions. Davies et al. (2007), looked at the effect of oxides of nitrogen on 334 ash trees, again in London and found a significant inverse relationship between epiphytic diversity and NO_x. However, the existence of a number of nitrogen tolerant species meant that a positive relationship was found between lichen abundance and NO_x. Of the 14 species of bryophyte recorded, 12 of them were recorded only in areas of low NO_x. It is probable that past conditions have meant that the time frame available to the bryophytes for colonisation is not simply the same as the length of time the tree has been growing for. In addition to this some areas of the tree, ie the trunks, are older than others, ie the branches, and so would be more affected by past atmospheric conditions.

There is also the possibility that changes in bark chemistry and tree structure provide better and more varied micro-habitats for bryophytes in larger, older trees (Rose, 1992). However, the data presented here suggest that this does not necessarily apply to orchards. The older habitat at Aldreth Road Aldreth 100, with smaller more closely spaced trees, proved to be bryologically poorer, both in species number and bryophyte cover, than the younger habitat. The youngest orchard, at Oaklands College, was found to host at least as many bryophyte species as much older orchards. However, much lower levels of bryophyte cover were recorded at Oaklands. Similarly, no clear link between tree age and number of epiphytic bryophytes was found by Robertson et al. (2012) where the 40 year old orchard was found to host 24 species of epiphytic bryophyte, in contrast to the 12 species recorded at an 80–100 year old orchard (Robertson et al., 2012). Immature trees, those younger than around 30 years, have been observed to be bryologically poor (Robertson et al., 2012; Stevenson and Rowntree, 2009). Current trends in commercial orchards necessitate the removal of apple trees after a relatively short period of time, which is not conducive to the establishment of bryophyte communities.

4.4. Orchard management factors affecting species diversity

The CCA identified trunk girth as being the most important factor in explaining the observed bryophyte distribution. This is not unexpected. A number of other studies have found phorophyte diameter to be of importance in the distribution of epiphytic bryophytes generally, Aude and Poulsen (2000) and of individual species (Kuusinen and Penttinen, 1999). In many studies, trunk girth is used as a proxy for tree age. However, this study has shown that in the case of these orchards, tree age is not a significant variable.

Almost as important in the analysis as trunk girth was the distance to nearest orchard tree with larger spacing being associated with more bryophyte cover and diversity. One of the reasons pasture-woodlands are so important to the conservation of epiphytic bryophytes and lichens is the large distance between the trees. Where this distance has been reduced by inter planting with new trees, for example at Savernake Forest in Wiltshire, a decrease in species diversity has been observed (Rose, 1992). However, the influence of tree density is not simply linear. Hazell et al. (1998) found that forest density had different impacts on bryophyte species with moisture loving species occurring more frequently on trees in denser stands. Trees in orchards are planted further apart in anticipation of their final size (Roach, 1956) and so there is some correlation between tree size and distance between trees. It is difficult then to distinguish between the effect of trees spaced further apart and trees with larger trunks. Within the analysis presented here some species, in particular *Brachythecium velutinum*, were found to show a preference for more densely planted trees with smaller trunk girths. Larger trees may be considered generally "better" for epiphytes overall, however they may not provide the optimum habitats for all species.

4.5. Conclusions

The variable, but generally high numbers of epiphytic bryophytes recorded in orchards makes them important habitats for these species to thrive.

The influence of orchard management is important in dictating the structure of these habitats. One aspect of management which makes these habitats unique is the control over the size and shape of the fruit trees, and it was this which was found to play a small, but significant role in the distribution of the epiphytic bryophytes in this study.

The conservation value of traditional orchards comes not only from the species that they can support but the way these habitats fit into the landscape. Small orchards can be found across the UK sometimes in relatively urban areas. These small areas can, if managed properly, provide a concentration of biodiversity provided the aspects of the habitats which are important to biodiversity can be identified. This study has shown that increased tree spacing and allowing trees to grow larger can provide a suitable habitat for epiphytic bryophytes to thrive.

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References

- Atherton, I., Bosanquet, S., Lawley, M., 2010. *Mosses and Liverworts of Britain and Ireland: A Field Guide*. British Bryological Society, Plymouth.
- Aude, E., Poulsen, R.S., 2000. Influence of management on the species composition of epiphytic cryptogams in Danish *Fagus* forests. *Appl. Veg. Sci.* 3, 81–88.
- Barkman, J.J., 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes*. Van Gorcum, Assen.
- Bates, J.W., 1992. Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, Western Scotland—a multivariate-analysis. *J. Ecol.* 80 (1), 163–179.
- Bates, J.W., Proctor, M.C.F., Preston, C.D., Hodgetts, N.G., Perry, A.R., 1997. Occurrence of epiphytic bryophytes in a 'tetrad' transect across southern Britain 1. Geographical trends in abundance and evidence of recent change. *J. Bryol.* 19, 685–714.
- Bates, J.W., Roy, D.B., Preston, C.D., 2004. Occurrence of epiphytic bryophytes in a 'tetrad' transect across southern Britain. 2. Analysis and modelling of epiphyte-environment relationships. *J. Bryol.* 26, 181–197.
- Burrough, A.E., Robertson, H.J., 2008. Traditional orchard survey - mapping England's traditional orchards. In: *Orchards and Groves: Their History, Ecology, Culture and Archaeology*. Sheffield Hallam University.
- Burrough, A.E., Oines, C.M., Oram, S.P., Robertson, H.J., 2010. Traditional orchard project in England—The creation of an inventory to support the UK habitat action plan. Natural England Commissioned Reports Number 077.
- Davies, L., Bates, J.W., Bell, J.N.B., James, P.W., Purvis, O.W., 2007. Diversity and sensitivity of epiphytes to oxides of nitrogen in London. *Environ. Pollut.* 146 (2), 299–310.
- Defra, 2013. Survey of orchard fruit October 2012—England and Wales. Downloaded from <https://www.gov.uk/government/statistics/orchard-fruit-survey-2012> on 02/09/2014.
- EIC, 2010. Extech Instruments Corporation Website Retrieved 02/09/2014, from <http://www.extech.com/instruments/product.asp?catid=40&prodid=430>.
- Greig-Smith, P., 1983. *Quantitative Plant Ecology*, third ed. Blackwell Scientific Publications, Oxford.
- Hammer, O., 1999. *PAleontological Statistics: Reference manual*. Natural History Museum, University of Oslo.
- Hazell, P., Kellner, O., Rydin, H., Gustafsson, L., 1998. Presence and abundance of four epiphytic bryophytes in relation to density of aspen (*Populus tremula*) and other stand characteristics. *Forest Ecol. Manag.* 107 (1–3), 147–158.
- Henderson, P., Seaby, R., 2008. *A Practical Handbook for Multivariate Methods*. Pisces Conservation Ltd., Lymington.
- Hill, M.O., Preston, C.D., Bosanquet, S.D.S., Roy, D.B., 2007. BRYOATT: Attributes of British and Irish Mosses, Liverworts and Hornworts. Centre for Ecology and Hydrology, Huntingdon.
- Hodgetts, N.G., Preston, C.D., Stevenson, C.R., 2006. *Antitrichia curtispindula* in a Cambridgeshire orchard. *Field Bryol.* 89, 8–10.
- Kershaw, K.A., Looney, J.H.H., 1985. *Quantitative and Dynamic Plant Ecology*, third ed. Edward Arnold, Ontario.
- Kiraly, I., Odor, P., 2010. The effect of stand structure and tree species composition on epiphytic bryophytes in mixed deciduous-coniferous forests of Western Hungary. *Biol. Conserv.* 143 (9), 2063–2069.
- Kuusinen, M., Penttinen, A., 1999. Spatial pattern of the threatened epiphytic bryophyte *Neckera pennata* at two scales in a fragmented boreal forest. *Ecography* 22 (6), 729–735.
- Larsen, R.S., Bell, J.N.B., James, P.W., Chimonides, P.J., Rumsey, F.J., Tremper, A., et al., 2007. Lichen and bryophyte distribution on oak in London in relation to air pollution and bark acidity. *Environ. Pollut.* 146 (2), 332–340.
- Lobel, S., Rydin, H., 2010. Trade-offs and habitat constraints in the establishment of epiphytic bryophytes. *Funct. Ecol.* 24 (4), 887–897.
- Lush, M., Robertson, H.J., Alexander, K.N.A., Giavarini, V., Hewins, E., Mellings, J., et al. 2009. Biodiversity studies of six traditional orchards in England (No. NERR025): Natural England.
- NE, 2008. Natural England: State of the Natural Environment Report. Retrieved 02/09/2014, from <http://www.naturalengland.org.uk/publications/publications/default.aspx>.
- PISCES, 2007. ECOM II: understanding relationships in nature. PISCES Conservation Ltd. Retrieved 09/01/2012 from [http://www.pisces-conservation.com/index.html?softcap.html\\$softwaremenu.html](http://www.pisces-conservation.com/index.html?softcap.html$softwaremenu.html).
- Roach, F.A., 1956. Planting systems and tree forms. In: Bush, R.G.W., Wallace, T. (Eds.), *Modern Commercial Fruit Growing*. Hazel, Watson and Viney Ltd., London.
- Robertson, H.J., Wedge, C., 2008. Traditional orchards and the UK biodiversity action plan. In: *Orchards and Groves: Their History, Ecology, Culture and Archaeology*. Sheffield Hallam University.
- Robertson, H., Marshall, D., Slingsby, E., Newman, G., 2012. Economic, biodiversity, resource protection and social values of orchards: a study of six orchards by the Herefordshire Orchards Community Evaluation Project. Natural England Commissioned Reports, Number 090.
- Rose, F., 1992. Temperate forest management: its effects on bryophyte and lichen floras and habitats. In: Bates, J.W., Farmer, A.M. (Eds.), *Bryophytes and Lichens in a Changing Environment*. Oxford Science Publications, Oxford.
- Seaby, R., Henderson, P., 2007. Community Analysis Package 4.0: searching for structure in community data. PISCES Conservation Ltd. Retrieved 09/01/2012 from [http://www.pisces-conservation.com/index.html?softcap.html\\$softwaremenu.html](http://www.pisces-conservation.com/index.html?softcap.html$softwaremenu.html).
- Smith, A.J.E., 1982. Epiphytes and epiliths. In: Smith, A.J.E. (Ed.), *Bryophyte Ecology*. Chapman and Hall, London, (Chapter 7).
- Smith, A.J.E., 2004. *The Moss Flora of Britain and Ireland*, second ed. Cambridge University Press, Cambridge.
- Stevenson, R., Rowntree, J., 2009. Bryophytes in East Anglian orchards. *Field Bryol.* 99, 10–18.