

Identifying substitute host tree species for epiphytes: The relative importance of tree size and species, bark and site characteristics

Ruth J. Mitchell¹  | Richard L. Hewison¹ | Joan Beaton¹ | John R. Douglass²

¹The James Hutton Institute, Aberdeen, UK

²Independent lichenologist, Stonehouse, South Lanarkshire, UK

Correspondence

Ruth J. Mitchell, The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK.
Email: Ruth.Mitchell@Hutton.ac.uk

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Abstract

Questions: Can bark characteristics be used to determine the suitability of trees to host epiphytic bryophytes and lichens or are other tree and site characteristics more important? Identification of substitute hosts is required in the face of epidemic tree deaths due to diseases that are a threat to affiliated epiphytic communities. We assess the suitability of seven phorophytes to host the epiphytes associated with the UK native oak species, *Quercus petraea* and *Quercus robur*, which are currently threatened by a range of pests and pathogens.

Location: Six botanic gardens and arboreta across the UK.

Method: We recorded the site, habitat, tree (height, diameter at breast height [1.3 m; DBH], percentage canopy cover) and bark characteristics (pH, conductivity, density, water-holding capacity, hardness, topography) and epiphytic community composition on *Acer pseudoplatanus*, *Castanea sativa*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus cerris*, *Quercus petraea*, *Quercus robur*, *Quercus rubra* and *Tilia × europaea*. In total 230 trees were surveyed across the six sites.

Results: Comparisons between all trees showed significant correlations between similarities in community composition and bark characteristics. However, “tree characteristics” (species, height, DBH and canopy over) explained more of the variation in epiphytic community composition than bark and site characteristics. Phorophytes with similar epiphytic community richness or composition to native oaks did not necessarily have similar bark characteristics. Non-native oaks and the non-native hybrid *Tilia × europaea* supported similar epiphyte communities to the native oaks and are suggested as substitute phorophytes.

Conclusion: Using bark traits is not a reliable method to assess the suitability of substitute phorophytes to conserve epiphytic communities. Instead, the epiphytes hosted by a wider range of phorophytes should be recorded to allow an assessment of their suitability as substitute hosts and hence aid management decisions on replacement phorophytes following tree loss.

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KEYWORDS

acute oak decline, bark pH, bryophytes, lichens, pathogens, pests, phorophytes, *Quercus*, substitute tree, tree disease, woodland resilience

1 | INTRODUCTION

Epidemic tree deaths due to disease have been described as “an insidious, mostly overlooked, threat to sessile affiliate communities” (Jonsson & Thor, 2012). Atmospheric pollution (Johnsen & Søechting, 1974; A.P.R.I.L., 2002) and land management (Stofer et al. 2006; Wolseley et al. 2006) have been known to influence the epiphytic community composition for many decades. More recently, tree diseases and climate change have also been identified as drivers of decline in epiphytic abundance and diversity (Ellis et al. 2012; Ellis et al. 2014; Hultberg et al. 2020). The decline of *Fraxinus excelsior* in the UK due to the tree disease ash dieback could have an impact on epiphytes equivalent to that of climate change in 2080 under a high emissions scenario (Ellis et al. 2014). Extirpation of epiphytes due to ash dieback has been recorded in Estonia (Löhmus & Runnel, 2014) and average epiphytic lichen coextinction probabilities in Sweden increased with lichen host specificity to *Fraxinus excelsior* (Jonsson & Thor, 2012). Many epiphytes threatened by tree diseases, because they grow mostly or exclusively on trees threatened by disease (e.g., *Fraxinus excelsior*) are species which were not currently red-listed or otherwise protected (Jonsson & Thor, 2012; Mitchell et al. 2014; Hultberg et al. 2020), suggesting that tree disease epidemics cause unforeseen threats to many species.

For all but obligate epiphytes (defined here as species found only on one tree species) the impacts of tree diseases can, at least partially, be mitigated by increasing the diversity of phorophytes within a stand, thus providing other hosts for the epiphytes (Ellis et al. 2014; Mitchell et al. 2014; Mitchell et al. 2019a). However, identification of suitable substitute hosts to support the threatened species is critical as different hosts will support different epiphytes (Mitchell et al. 2014; Mitchell et al. 2019a). Substitute host trees are phorophytes, other than the tree species threatened by disease, which are known to host the epiphyte. One way to assess the suitability of substitute phorophytes is to use existing national biodiversity records where the epiphyte substrate has been recorded; the proportion of records of any given epiphyte on a given phorophyte representing the suitability of that phorophyte (Mitchell et al. 2014; Mitchell et al. 2019a). However, surveyors traditionally record the epiphytes found on native trees more often than those on non-native trees and the lack of epiphyte records from non-native tree species was identified as a major knowledge gap (Mitchell et al. 2017; Mitchell et al. 2019a). If the tree traits controlling epiphytic community composition can be identified then it would be possible to identify substitutes with similar traits, aiding conservation managers.

Epiphytes are known to be influenced by bark pH (Barkman, 1958; Kuusinen, 1996), bark structure (Barkman, 1958),

water-holding capacity (Callaway et al. 2002), tree species (Kubiak & Osyczka, 2019), management and surrounding habitat (Juriado et al. 2009; Mežaka et al. 2012; Kubiak & Osyczka, 2020), but the relative importance of these characteristics in identifying suitable substitute phorophytes is unknown. Here, we assess the suitability of seven phorophytes to support the epiphytic lichens and bryophytes found on the native British oak species *Quercus petraea* and *Quercus robur*. *Quercus petraea/robur* are the UK’s most common native trees (Forestry Commission, 2003) and, as in most of Europe, are at risk from Acute Oak Decline (Denman et al. 2014), Chronic Oak Decline (Denman & Webber, 2009), Oak Processionary Moth (Tomlinson et al. 2015) and a variety of powdery mildews (Lonsdale, 2015). The substitute phorophytes assessed include two native tree species: *Fraxinus excelsior* and *Fagus sylvatica*, although the latter is thought not to be strictly native in western and northern Britain, and two non-native but naturalized species: *Acer pseudoplatanus* and *Castanea sativa*. These four species occur naturally in oak woods in the UK (Rodwell, 1991) and might be expected to fill canopy gaps created by the loss of *Quercus petraea/robur*. In addition, we assess the suitability of one non-native hybrid, *Tilia × europaea*, and two non-native *Quercus* species, *Quercus cerris* and *Quercus rubra*, which are known to grow in the same conditions (climate and soils) as *Quercus petraea/robur* (Pyatt et al. 2001). The non-native oaks belong to different taxonomic sections than the British native oaks and so may be resistant to, or tolerant of, diseases affecting native oaks. *Fraxinus excelsior* is not a viable alternative to *Quercus petraea/robur* in the UK as its population is declining due to ash dieback. However, as it supported the greatest number of oak-associated lichen and bryophytes in an assessment of 30 substitute phorophytes using national biodiversity records (Mitchell et al. 2019b), it is included here as it may provide evidence about the key bark traits determining host suitability.

In the UK *Quercus petraea/robur* is known to host 716 lichen species and 229 bryophyte species (Mitchell et al. 2019b). All the oak-associated bryophytes are known to be cosmopolitan (i.e. occurring on a wide range of other phorophytes). Of the oak-associated lichens 12 are obligate (only found on oak; Mitchell et al. 2019b) and 190 are preferentially found on oak (highly- and partially-associated lichens as classified by Mitchell et al. 2019b), which are lichens either rarely found on tree species other than oak or lichens that use oak more frequently than its availability). Thus, a decline in oak could have a significant impact on the epiphytic lichen flora of the UK. While a large decline in oak is not imminent, older trees support more epiphytes (Nordèn et al. 2018; Mitchell et al. 2019a), thus planning many decades ahead to provide suitable substitute phorophytes at the correct growth stage is required.

While using oak and our seven potential substitute phorophytes as a case study, the concept of studying phorophyte characteristics to assess their suitability to act as substitute hosts has applicability across the entire range of threatened tree species. Specifically, we aim to answer the following questions: (1) how similar are the bark characteristics, epiphyte species richness and epiphyte community composition between oak and the seven possible replacement phorophytes? We hypothesize that tree species similar to native oaks in bark characteristics would support an epiphyte community similar to the native oaks. (2) Which bark characteristics influence the number of oak-associated lichen and bryophyte species present? (3) Do tree size and species, bark characteristics, surrounding habitat or site most strongly influence the community composition of oak-associated lichens and bryophytes on substitute phorophytes?

2 | METHODS

2.1 | Site selection

Six garden or parkland sites in rural locations with low pollution levels were selected from across the UK (Table 1). The sites were previously the large formal gardens or parklands of country manor houses, that due to historical management had a selection of old trees (usually more than 150 years old), and are now managed as botanic gardens and arboreta. The sites were chosen to have as many

as possible of the following species: *Acer pseudoplatanus*, *Castanea sativa*, *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus cerris*, *Quercus petraea*, *Quercus robur*, *Quercus rubra*, *Tilia × europaea*. Between 35 and 40 trees were recorded at each site with 230 trees sampled in total (Table 2). The trees sampled were “standard” trees, pollarded specimens were avoided to increase standardization.

2.2 | Lichen and bryophytes

The identity of all lichen and bryophyte species on the trunk, from ground level to 1.75 m, were recorded; this being the height that could safely be surveyed from ground level. In addition, lichens present on the branches and twigs (referred to collectively as branches) were recorded where these could be safely reached from the ground, i.e. branches within 1.75 m of the ground. It is acknowledged that these data will, of necessity, be incomplete. Most of the lichens were identified in the field using a $\times 10$ illuminating hand lens (Lichen candelaris Pattersons Elektronik AB, Uppsala, Sweden). Chemical spot tests on lichen thalli were used to confirm identification (Orange et al. 2001). The “C” test used household bleach not containing sodium hydroxide; the active ingredient was sodium hypochlorite. The “K” test used 10% caustic soda mixed with 90% water; the active ingredient was sodium hydroxide. The “PD” test used Steiner's solution; the active ingredient was *para*-phenylenediamine (1,4-phenylenediamine). Specimens that could not be identified in the field were collected

TABLE 1 Details of site locations, soil type, climate and pollution

	Site					
	Bodnant National Trust garden	Crathes National Trust for Scotland Garden	Dinefwr National Trust garden	Knights Hayes National Trust Garden	Mount Stuart Garden	Westonbirt Arboreta
Country	Wales	Scotland	Wales	England	Scotland	England
Latitude	53.23	57.05	51.88	50.92	55.79	51.61
Longitude	-3.79	-2.42	-4.01	-3.47	-5.02	-2.21
Total area (ha)	32	100	350	106	40	240
Altitude (m)	0–70	50–100	30–100	100–165	0–50	120–140
Soil type	Clay, acid	Acid	Acid	Acid red brown soil	Acid	Loam, alkaline and acid
General aspect	South and West	Southerly	South-westerly	Easterly	Easterly	Mostly flat
Average annual rainfall (mm)	1,100	780	1,323	1,065	1,455	840
Average daily maximum temperature (°C)	13.7	12.2	14.2	12.6	12.5	13.4
Average daily minimum temperature (°C)	7.6	3.5	6	6.1	6.4	5.6
Nitrogen deposition (kg N/ha/year)	27.16	17.92	27.3	34.72	13.16	29.82
Sulphur dioxide concentration $\mu\text{g m}^{-3}$	0.64	0.44	0.95	1.1	0	0.79

Note: Climate data are from 1981–2010 taken from the nearest UK Meteorological station all of which were < 20 km away from the site. Pollution data are from 2016–2018, source: the Air Pollution Information System <http://www.apis.ac.uk/>.

TABLE 2 The number of trees of each species sampled at each site

Tree species	Sites						Total
	Bodnant	Crathes	Dinefwr	Knighthayes	Mount Stuart	Westonbirt	
<i>Acer pseudoplatanus</i>	6 (6)	5 (4)	6 (6)	4 (4)	6 (0)	5 (5)	32 (25)
<i>Castanea sativa</i>	4 (4)		6 (5)	4 (4)	5 (2)	5 (4)	24 (19)
<i>Fagus sylvatica</i>	5 (5)	8 (8)	6 (6)	5 (5)	6 (3)	5 (5)	35 (32)
<i>Fraxinus excelsior</i>	4 (2)	6 (5)	7 (7)	5 (5)	5 (3)	5 (4)	32 (26)
<i>Quercus cerris</i>				7 (7)	2(1)	5 (4)	14 (12)
<i>Quercus petraea</i>	8 (7)	5 (4)					13 (11)
<i>Quercus robur</i>	3 (2)	6 (5)	7 (6)	6 (6)	6 (2)	6 (5)	34 (26)
<i>Quercus rubra</i>	5 (3)			4 (4)	2 (2)	4 (4)	15 (13)
<i>Tilia × europaea</i>	5 (5)	5 (3)	5 (5)	5 (5)	6 (2)	5 (5)	31 (25)
Total	40	35	37	40	38	40	230 (189)

Note: The number of trees where it was possible to sample the branches is given in parentheses.

using a small knife. Morphological features were then observed under a dissecting microscope and microscopic features (including spores) were assessed using a compound microscope.

2.3 | Tree characteristics and surrounding habitat

For each tree, diameter at breast height (DBH, 1.3 m above the ground) was measured and the height of the tree measured using a clinometer (Suunto Opti Height Meter Clinometer PM-5 Suunto, Vantaa, Finland). Canopy cover and “habitat structure” were recorded in the four cardinal sectors around the tree. Canopy cover was measured using a spherical densiometer (Model-A Forestry Supplies Inc. Jackson, US; Lemon, 1956) and the average cover across the four sectors calculated. Within each sector the distance to the nearest tree (up to a maximum of 30 m away), its species and DBH of the tree was recorded. The DBH of the nearest tree divided by the distance, summed for the four sectors provided a measure of the closeness and size of surrounding trees and was termed “habitat structure.” The surrounding habitat of the tree was recorded as “shaded semi-natural woodland,” “open grassland-parkland” or “garden with shrubs/plants” (see Appendix S1 for details).

2.4 | Bark characteristics

On each cardinal aspect of the trunk, a 30 cm × 30 cm quadrat was placed at one of four randomly allocated heights (low 0.5–0.8 m, lower-middle 0.8–1.1 m, upper-middle 1.1–1.4 m, upper 1.4–1.7 m above ground level). Within each quadrat the following measurements were made. The bark pattern was classified as smooth, fissured, flaky, rugose or patterned (see Appendix S2 for details). If fissures were present, the width and depth of eight randomly selected furrows and the width of eight ridges were measured. Bark

hardness was measured using a durometer (Tire Durometer Type A ASTM 2,240 Shore Type X.F) with eight random measures per quadrat.

Small bark samples (c. 2 cm × 2 cm) were taken from each tree. On return to the lab, the samples were air dried at 30°C and any epiphytes or surface debris removed with a small wire brush. The bark was cut into small chunks of c. 5 mm³, with half used for bark density following the method in Ellis et al. (2015) while the remaining half was ball-milled (MM22 Mixer Mill, Retsch), mixed with distilled water at a ratio of 1:20 and left for 24 hr before pH and conductivity were measured.

2.5 | Data processing

The median width of the bark furrows and ridges, and median furrow depth in each quadrat, was calculated and used to calculate bark topography (Bt) following the method in Ellis and Coppins (2007). Bt provides an index of surface roughness, but could yield high values even if the absolute depth of furrows is small, if the furrows account for a relatively large area compared to the ridges (Ellis et al. 2015); therefore furrow depth was analysed in addition to Bt.

Species nomenclature follows the British Bryological Society (2019) for bryophytes and The British Lichen Society (2019) for lichens; all authorities are listed in Appendices S3–S5. Only those epiphytes known to be associated with *Quercus petraea/robur* in the UK, as identified by Mitchell et al. (2019b), were included in the analysis to avoid including obligate epiphytes from other tree species in assessments of similarity to oak. The data were further subdivided by identifying those species that are preferentially associated with oak and thus most at risk of extirpation should oak decline in abundance (Mitchell et al. 2019a). The analysis of species richness and composition described below was carried out separately for (a)

all oak-associated (OA) lichens on the trunks, (b) all preferentially oak-associated (POA) lichens on the trunks, (c) all OA lichens on the branches, (d) all POA lichens on the branches, and (e) all OA bryophytes on the trunk (there are no preferentially oak-associated bryophytes; Mitchell et al. 2019a).

2.6 | Data analysis

All data analyses other than the partial Canonical Correspondence Analysis (pCCA; see below), were carried out within R version 3.6.2 (R Core Team, 2018). In all univariate analyses, site was included as a random effect to account for the fact that groups of trees occurring together, even if different species, with different bark traits, may tend to have more similar communities than other groups of trees at different sites, because of a shared species pool, history of colonisation and differences in site pollution levels, climate and soil type (Table 1). In all multivariate analyses a pseudo-species of “none” was created for trees with no preferentially associated species to enable them to be included in the analysis.

To test if tree species differed in their bark characteristics, linear mixed-effects models were used to test the relationship between the bark chemistry and physical properties (the dependent variables) and tree species (included as a fixed effect) and DBH (included as a continuous variable) using the *lmerTest* package in R (Kuznetsova et al. 2017). Tree and quadrat were included as random effects, in addition to site, where there were multiple measurements per tree and/or quadrat. To meet assumptions of normality of residuals, bark conductivity was log-transformed and furrow depth was square-root-transformed. ANOVA type III tables and Satterthwaite methods for denominator degrees of freedom were used for *F*-tests. Tukey's pairwise comparisons were used to determine differences between pairs of tree species and *p*-values were adjusted using the Tukey correction method for multiple tests (Lenth, 2019).

To assess if tree species differed in their lichen and bryophyte species richness (number of lichen/bryophyte species) generalized linear mixed-effect models with a Poisson distribution using the *glmer* function within *lme4* (Bates et al. 2015) were used. The effect of tree species on lichen and bryophyte species richness was assessed after the effect of DBH had been taken into account, DBH representing the age and size of the tree and hence the time available for colonization by epiphytes to occur and the area available to host epiphytes. Generalized linear mixed-effects models were also used to assess if the bark characteristics influenced lichen and bryophyte species richness. The independent variables were DBH and the following bark characteristics: density, pH, conductivity, topography, median furrow depth, water-holding capacity, hardness. Each variable was tested after taking account of the other variables.

Similarity between trees in bark chemical/physical characteristics and epiphytic community composition was calculated using a similarity index of one minus the Bray–Curtis dissimilarity in *vegdist* within *Vegan* (Oksanen et al. 2019). The bark chemical/physical data were first standardized and normalized due to differences in

units between characteristics. For the community composition, the Bray–Curtis dissimilarity reduces to the Sørensen dissimilarity index as it is presence/absence data (Ricotta & Podani, 2017). Mantel tests were used to measure the correlation between the two similarity matrices (bark chemical/physical properties and community composition) using the “ade4” function with the Pearson correlation (Dray & Dufour, 2007). The similarity index for each tree against each *Quercus robur* and *Quercus petraea* tree was then extracted from the similarity matrix and used as the dependent variable in a linear mixed-effects model to test the effect of tree species on similarity to *Quercus robur* or *Quercus petraea*. Tree species was included as a fixed effect, and there were two random effects: “Site1” to indicate the site of the tree being compared and “Site2” to indicate the site of the oak against which the tree was compared.

Variation partitioning using pCCA in Canoco v5.12 (Ter Braak & Smilauer, 2012) was used to calculate the variation in community composition explained by four groups of explanatory variables. Group 1 “bark characteristics” contained bark pH, conductivity, bark density, water-holding capacity, bark hardness (average across quadrats), bark topography (average from the four quadrats) and median furrow depth. Bark topography was set to zero for trees with no fissures. Group 2 “tree characteristics” included height, DBH, percentage canopy cover (average from the four sectors) and tree species. Group 3 “site” included all six sites as categorical variables and Group 4 “habitat” included habitat structure and whether the site was grassland/parkland, garden or woodland.

3 | RESULTS

3.1 | Bark characteristics

Bark chemical and physical properties differed significantly between trees: bark hardness ($F_{8,217} = 28, p < 0.001$), bark density ($F_{8,217} = 27, p < 0.001$), water-holding capacity ($F_{8,216} = 15.8, p < 0.001$), bark pH ($F_{8,208} = 63.4, p < 0.001$) and bark conductivity ($F_{8,217} = 16.9, p < 0.001$; Figure 1). The two native oaks did not differ from each other in their chemical and physical properties but differed from the non-native oaks. Native oaks had greater water-holding capacity than *Quercus cerris* and lower density than *Quercus rubra* but were similar in terms of the other characteristics measured (Figure 1). Native oaks differed from all the non-*Quercus* species assessed in at least two and often three of the five chemical and physical bark characteristics measured.

Comparison of those phorophytes that had fissures (*Castanea sativa*, *Fraxinus excelsior*, *Quercus cerris*, *Quercus petraea*, *Quercus robur*, *Quercus rubra* and *Tilia × europaea*) showed significant differences in bark topography ($F_{6,147} = 12, p < 0.001$) and furrow depth ($F_{6,145} = 16, p < 0.001$). The native oak species did not differ from each other or from *Quercus cerris* in terms of bark structure but differed from *Quercus rubra* which had smoother bark topography and shallower furrow depth than the native oaks (Table 3, Figure 2). The native oaks did not differ from *Castanea sativa* and *Fraxinus excelsior*

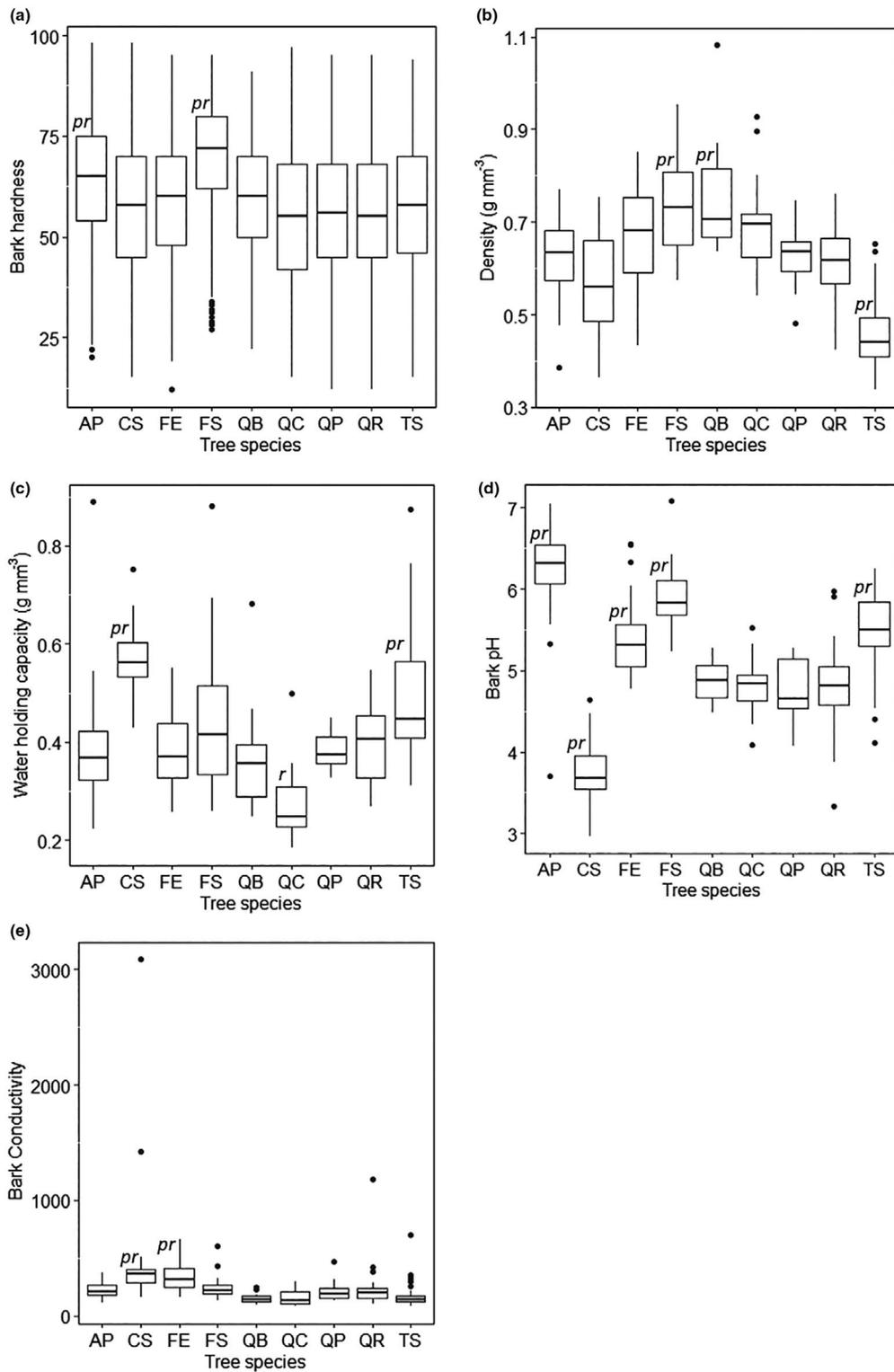


FIGURE 1 Boxplots of the physical and chemical properties of the bark of nine tree species: (a) hardness; (b) density; (c) water-holding capacity; (d) pH; and (e) conductivity. Box plots show the median, the 25th and 75th percentiles and whiskers (defined as the largest [or smallest] value no further than $1.5 \times$ the inter-quartile range). Data beyond the end of the whiskers are plotted individually. AP = *Acer pseudoplatanus*; CS = *Castanea sativa*; FS = *Fagus sylvatica*; FE = *Fraxinus excelsior*; QC = *Quercus cerris*; QP = *Quercus petraea*; QR = *Quercus robur*, QB = *Quercus rubra*; TS = *Tilia \times europaea*. The letters p and r indicate significant differences ($p < 0.05$) between the tree species and *Quercus petraea* or *Quercus robur* respectively, as assessed using Tukey's pairwise comparisons

but did differ from *Tilia × europaea* which has smoother bark and shallower furrows.

The similarity index, a multivariate assessment across all bark characteristics, showed substitute phorophytes differed in the similarity of their bark characteristics to *Quercus robur* ($F_{6,6165} = 1.949$; $p < 0.0001$) and *Quercus petraea* ($F_{6,2346} = 611$; $p < 0.0001$). *Fraxinus excelsior* and *Quercus cerris* were most similar to both species of native oak while *Acer pseudoplatanus* and *Fagus sylvatica* were least similar (Appendix S6).

3.2 | Oak-associated lichen species: trunk

One hundred and ninety-seven lichen species were recorded on the trunks, of which 181 were classified as OA lichens and 58 as POA (Appendix S3). *Pyrrhospora quereana*, *Dendrographa decolorans*, *Cliostomum griffithii*, *Flavoparmelia caperata*, *Lecanactis abietina* and *Chrysothrix candelaris* were the most frequent POA lichens. *Pyrrhospora quereana* was recorded on 144 trees across all phorophytes. The other five lichens occurred on at least 55 trees and were hosted by all phorophytes studied other than for *Pertusaria hymenea* (not found on *Quercus cerris*) and *Chrysothrix candelaris* (not found on *Fagus sylvatica*). Six PAO species were only recorded on *Quercus petraea* and/or *Quercus robur*: *Agonimia octospora*, *Chaenotheca chrysocephala*, *Chaenothecopsis savonica*, *Calicium salicinum*, *Mycobilimbia epixanthoides* and *Inoderma subabietinum* (Appendix S3). *Lepraria finkii*, *Lecanora expallens*, *Phlyctis argena*, *Lepraria incana*, *Lecanora chlarotera* and *Melanelixia glabrata* were the most common cosmopolitan OA lichens occurring on between 75 and 135 trees and on all tree species (Appendix S3). There were two lichen species listed by Mitchell et al. (2019b) as cosmopolitan in their association with oak which were only found on *Quercus petraea* and/or *Quercus robur*: *Chaenotheca brachypoda* and *Usnea subfloridana*.

There were significant differences between phorophytes in species richness of OA lichens ($\chi^2_8 = 49$, $p < 0.0001$) and POA lichens ($\chi^2_8 = 59.5$, $p < 0.0001$). Native oaks had greater species richness of OA lichens than *Castanea sativa*, *Quercus cerris* and *Tilia × europaea*

(Figure 3). Species richness of POA lichens was also greater on native oaks than on the substitute phorophytes except for the two non-native oaks and *Tilia × europaea*.

Substitute phorophytes differed in the similarity of their hosted OA lichen (*Quercus robur*: $F_{6,6174} = 50$, $p < 0.001$; *Quercus petraea*: $F_{6,2307} = 13$, $p < 0.001$) and PAO lichen (*Quercus robur*: $F_{6,6199} = 20$, $p < 0.001$; *Quercus robur*: $F_{6,2345} = 6.8$, $p < 0.001$) communities to those of native oaks. The two non-native oaks and *Tilia × europaea* were most similar to native oaks, although their relative ranking varied depending on which native oak species was being compared and which lichen group; OA or POA lichens (Table 3, Appendix S7).

3.3 | Oak-associated lichen species: branches

One hundred and thirty-seven lichen species were recorded on the branches of the 189 trees for which a survey was possible (Table 2). One hundred and twenty-five of these lichens were classed as OA lichens (Appendix S4), of which 19 were POA lichens. *Flavoparmelia caperata* was the most frequent POA lichen, occurring on the branches of 87 trees, and on all phorophytes. The POA species *Pertusaria hymenea*, *Punctelia reddenda* and *Anisomeridium bifforme* occurred on the branches of between 22 and 11 trees, but did not occur on all phorophytes. The remaining POA species were found on less than 10 trees. *Bryoria fuscescens*, *Cladonia polydactyla*, *Fellhanera bouteillei*, *Halecania viridescens* and *Opegrapha multipuncta*, all listed as cosmopolitan OA species by Mitchell et al. (2019b), were only found on the branches of *Quercus robur*.

Phorophytes differed in their species richness of OA lichens ($\chi^2_8 = 22.1$, $p < 0.01$) but pairwise comparisons showed no significant difference between native oaks and any of the substitute phorophytes. There was no significant difference between phorophytes in the species richness of POA lichens.

Substitute phorophytes differed in the similarity of their OA lichen (*Quercus robur*: $F_{6,3937} = 21$, $p < 0.001$; *Quercus petraea*: $F_{6,1661} = 12$, $p < 0.001$) and POA lichen (*Quercus robur*: $F_{6,3929} = 3.8$, $p < 0.01$; *Quercus petraea*: $F_{6,1661} = 4.6$, $p < 0.001$)

TABLE 3 The rank order of similarity of substitute phorophytes to native oaks in term of their epiphyte community composition

Tree part/ species group	Compared to	Level of community association with oak	
		Oak-associated	Preferentially oak-associated
Trunk/ lichens	<i>Quercus robur</i>	QC ^{df} > TS ^{ef} > QB ^{be} > CS ^b > FE ^c > FS ^{ac} > AP ^a	QC ^{ac} > TS ^{ac} > QB ^{ce} > AP ^{ef} > FE ^{bef} > CS ^{bdf} > FS ^d
	<i>Quercus petraea</i>	TS ^a > QB ^{ac} > QC ^{ac} > CS ^{bcd} > FE ^{bd} > FS ^{bd} > AP ^{bd}	TS ^c > QB ^{bc} > QC ^{bc} > AP ^{bc} > FE ^{bc} > FS ^{ab} > CS ^a
Branches/ lichens	<i>Quercus robur</i>	FS ^a > TS ^a > QC ^b > QB ^b > AP ^b > FE ^b > CS ^b	QB ^{ac} > TS ^c > QC ^{abc} > AP ^{abc} > CS ^{abc} > FS ^b > FE ^{bc}
	<i>Quercus petraea</i>	TS ^b > FS ^b > QC ^{bc} > QB ^{bc} > CS ^{acd} > AP ^{acd} > FE ^{ad}	FE ^b > FS ^{bc} > AP ^{bc} > QB ^{ab} > CS ^{ab} > QC ^{ac} > TS ^a
Trunk/ bryophytes	<i>Quercus robur</i>	FS ^b > TS ^b > QC ^{bd} > FE ^{cd} > QB ^c > AP ^c > CS ^a	N/A
	<i>Quercus petraea</i>	QC ^f > FS ^f > TS ^{bf} > QB ^{bd} > FE ^{de} > AP ^{ce} > CS ^{ac}	N/A

Abbreviations: AP = *Acer pseudoplatanus*; CS = *Castanea sativa*; FS = *Fagus sylvatica*; FE = *Fraxinus excelsior*; QC = *Quercus cerris*; QP = *Quercus petraea*; QR = *Quercus robur*; QB = *Quercus rubra*; TS = *Tilia × europaea*. Similarity was calculated as one minus the Sørensen dissimilarity index and ranking based on modelled mean estimates from linear mixed effects models, with site as a random effect. Phorophytes that are significantly different in their similarity to *Q. robur/petraea* have different superscripts, as assessed using Tukey's pair-wise comparisons adjusted for multiple tests. See Appendices S7 and S8 for data.

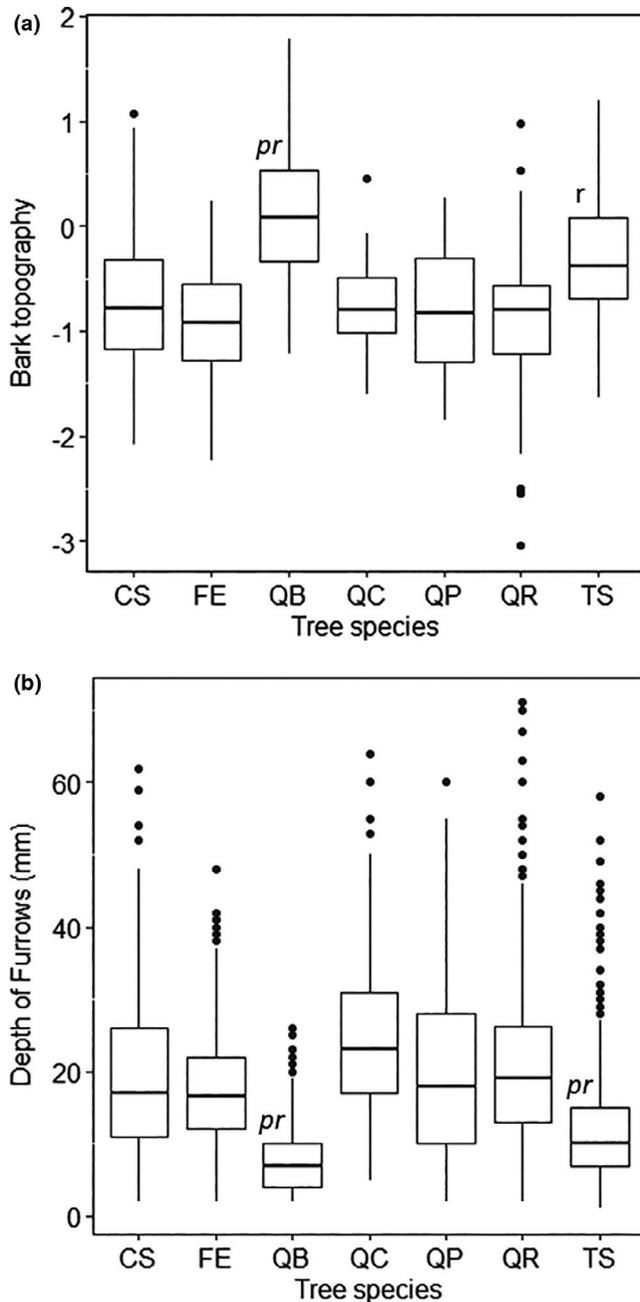


FIGURE 2 Boxplots of the bark structure for the trees that had fissures. (a) Bark topography; (b) depth of furrows. Box plots details as per Figure 1. AP = *Acer pseudoplatanus*; CS = *Castanea sativa*; FS = *Fagus sylvatica*; FE = *Fraxinus excelsior*; QC = *Quercus cerris*; QP = *Quercus petraea*; QR = *Quercus robur*, QB = *Quercus rubra*; TS = *Tilia × europaea*. The letters p and r indicate significant differences ($p < 0.05$) between the tree species and *Quercus petraea* or *Quercus robur* respectively, as assessed using Tukey's pairwise comparisons

communities to those on native oaks. The ranking of the substitute phorophytes differed substantially between the OA community and the POA community (Table 3, Appendix S7). For example, *Fagus sylvatica* and *Tilia × europaea* were most similar to *Quercus robur* with respect to the OA lichen community but *Quercus rubra* and *Tilia europaea* were most similar with respect to PAO lichens.

3.4 | Oak-associated bryophyte species

Sixty-five bryophytes were recorded, 56 of which are OA (Mitchell et al. 2019c, Appendix S5). *Hypnum cupressiforme* var. *resupinatum*, *Metzgeria furcata* and *Isothecium myosuroides* were the most frequently occurring OA bryophytes, occurring on more than 120 trees and on all phorophytes. *Brachythecium rutabulum* and *Kindbergia praelonga* were the only other species to be found on all tree species. There were no bryophytes that were only found on *Quercus robur* or *Quercus petraea*. Phorophytes differed in OA bryophyte species richness ($\chi^2_8 = 52$, $p < 0.0001$). The only difference between native oaks and the other phorophytes was between *Quercus robur* and *Fraxinus excelsior*, with *Fraxinus excelsior* having greater species richness (Figure 3).

Substitute phorophytes differed in the similarity of their hosted OA bryophyte community to *Quercus robur* ($F_{6,6195} = 69$, $p < 0.001$) and *Quercus petraea* ($F_{6,2361} = 30$, $p < 0.001$). *Fagus sylvatica* and *Tilia × europaea* hosted the most similar bryophyte community to *Quercus robur*. *Quercus cerris*, *Quercus robur* and *Fagus sylvatica* hosted the most similar communities to those found on *Quercus petraea* (Table 3, Appendix S8). The bryophyte communities on *Acer pseudoplatanus* and *Castanea sativa* were least similar to those hosted by native oaks.

3.5 | Relating the epiphytic community to bark characteristics

Bark density ($\chi^2_1 = 7.6$, $p < 0.01$) and pH ($\chi^2_1 = 7.6$, $p < 0.01$) were significant in determining OA lichen richness but furrow depth ($\chi^2_1 = 7.1$, $p < 0.01$) was the only bark characteristic that was significant in determining the richness of POA species. Trees with denser and more alkaline bark had more OA lichens while trees with deeper furrows had a greater number of POA species. OA bryophyte richness was influenced by bark pH ($\chi^2_1 = 28.4$, $p < 0.01$), conductivity ($\chi^2_1 = 11$, $p < 0.01$) and hardness ($\chi^2_1 = 8.3$, $p < 0.01$), trees with softer and more alkaline bark having greater species richness.

Mantel tests showed significant correlations between the bark chemical/physical properties and community composition. However, the strength of these correlations, as assessed by the Mantel r statistic was weak: OA lichens ($p = 0.001$, $r = 0.1625$), POA lichens ($p = 0.001$, $r = 0.08651$), bryophytes ($p = 0.001$, $r = 0.08251$).

3.6 | Relating lichen and bryophyte trunk community composition to bark, tree and site characteristics

The pCCA analyses of the OA and POA lichen and OA bryophyte communities showed similar patterns, with all variables together explaining between 21% and 24% of the variation (Table 4). The bark characteristics alone explained between 6% and 7% of the variation in the lichen and bryophyte communities (Table 4). Tree

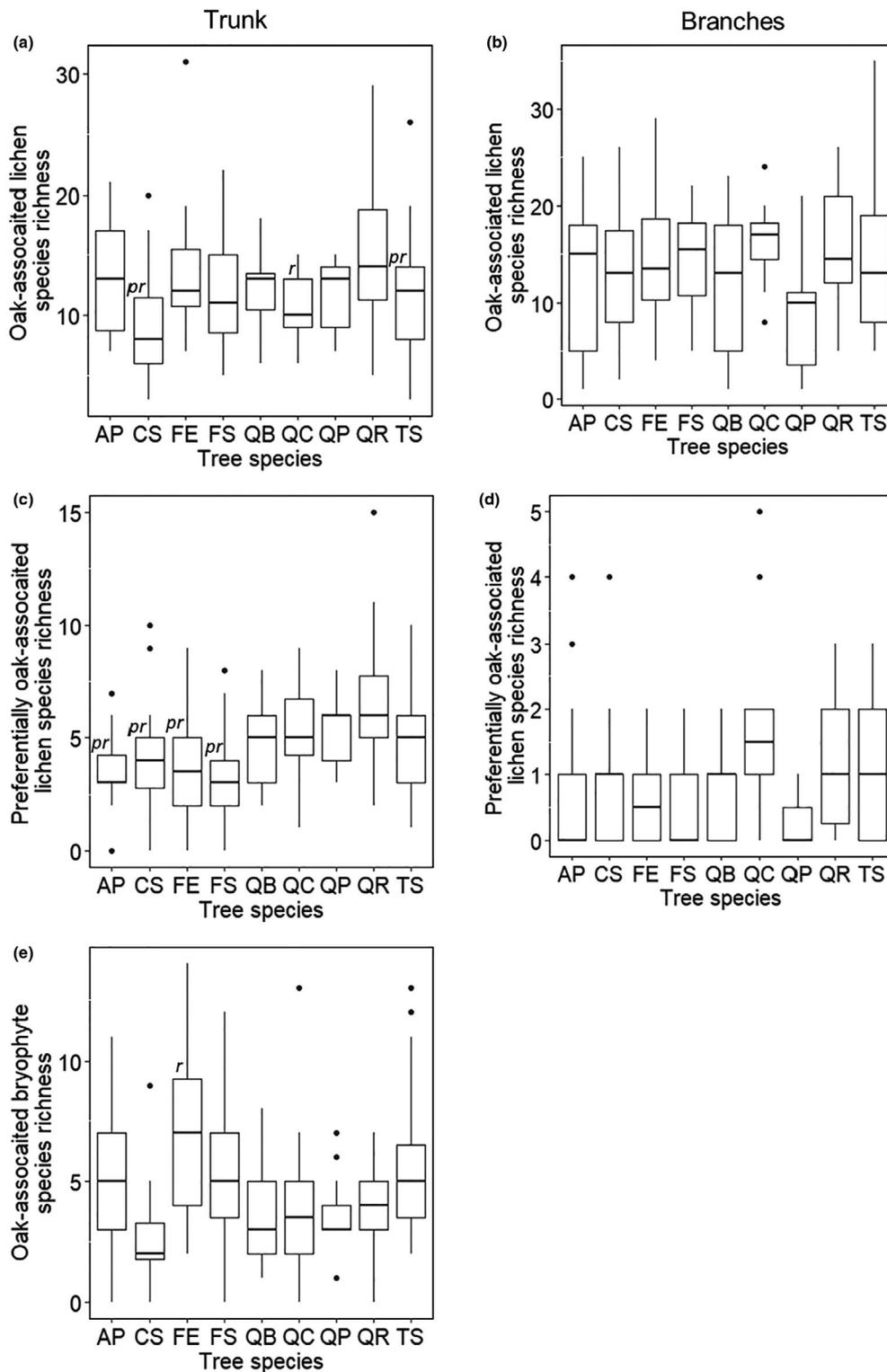


FIGURE 3 Boxplots of the species richness of oak-associated epiphytes of nine tree species: (a) all oak-associated lichens on the trunk; (b) all oak-associated lichens on the branches; (c) preferentially oak-associated lichens on the trunk; (d) preferentially oak-associated lichens on the branches; and (e) oak-associated bryophytes. Box plots details as per Figure 1. AP = *Acer pseudoplatanus*; CS = *Castanea sativa*; FS = *Fagus sylvatica*; FE = *Fraxinus excelsior*; QC = *Quercus cerris*; QP = *Quercus petraea*; QR = *Quercus robur*, QB = *Quercus robur*; TS = *Tilia × europaea*. The letters p and r indicate significant differences ($p < 0.05$) between the tree species and *Quercus petraea* or *Quercus robur* respectively, as assessed using Tukey's pairwise comparisons

characteristics, which explained 10% and 11% of the variation in the data only explained 2–3% of the same variation as the bark characteristics, with less overlap for PAO lichens than OA lichens. Habitat explained 2–3% of the variation and site 6–11%, with site being more important for lichens than for bryophytes (Table 4).

4 | DISCUSSION

4.1 | Do tree species with bark characteristics similar to native oaks support the greatest number of oak-associated lichens/bryophytes?

The results provided only limited evidence to support the hypothesis that phorophytes similar in their bark characteristics to native oaks would support a similar epiphytic community. Comparisons between all trees (Mantel tests) showed significant correlations between similarities in community composition and bark characteristics, although the strength of these relationships was weak. Comparisons of substitute phorophyte similarities to oak, rather than across all species as with the Mantel test, showed that not all phorophytes with similar epiphytic communities to oak had similar bark characteristics. *Quercus cerris*, for example, supports our hypothesis, as it had the most similar bark to the native oaks (differing from *Quercus robur* in only one of the seven bark characteristics measured and not differing from *Quercus petraea*), was not different from the native oaks in terms of POA lichen richness and was ranked in the top three phorophytes with the most similar epiphytic communities (Table 3). In contrast *Tilia × europaea* differed from the native oaks in five (*Quercus robur*) or four (*Quercus petraea*) of the seven bark characteristics measured (Figures 1 and 2) but, like *Quercus cerris*, did not differ from the native oaks in terms of preferentially oak-associated lichen richness and was ranked in the top three phorophytes with the most similar epiphytic communities (Table 3).

There was some evidence that the bark characteristics that are important in determining the lichen community species richness differ when considering POA species rather than all OA species. Trees with denser and more alkaline bark had more OA lichens, while trees with deeper furrows had a greater number of POA. Thus, the desirable characteristics of substitute phorophytes may differ depending on the conservation objectives and if priority is given to POA species.

4.2 | The importance of tree characteristics

One of the aims of this work was to assess the importance of bark, tree, habitat and site characteristics in identifying suitable substitute phorophytes to help conserve epiphytic communities in the face of tree species loss. Tree characteristics which included height, DBH, percentage canopy cover and tree species, rather than any of the measured characteristics of bark, the surrounding habitat or site, were found to be the biggest factor influencing

TABLE 4 Variation in lichen and bryophyte communities explained by four groups of variables: bark characteristics, tree characteristics, habitat and site and the overlap (η) in the variation explained between pairs of these groups

Explanatory variable group	All oak-associated lichens	Preferentially oak-associated lichens	Oak-associated bryophytes
All groups	22.7	24.0	20.87
Bark	6.92	6.26	6.82
Tree	11.33	11.09	10.75
Habitat	2.70	3.13	2.21
Site	8.22	10.9	5.96
Bark η tree	3.12	2.26	2.96
Bark η habitat	0.43	0.56	0.13
Bark η site	0.89	1.38	0.56
Tree η habitat	1.90	1.19	0.56
Tree η site	1.40	2.65	0.79
Habitat η site	0.80	1.23	0.15

Note: The data are the results from variation partitioning using partial Canonical Correspondence Analysis. The group “bark characteristics” contained the variables bark pH, conductivity, bark density, water-holding capacity, bark hardness, bark topography and median furrow depth. “Tree characteristics” included height, DBH, percentage canopy cover. The group “site” included all six sites as categorical variables and the “habitat” group included habitat structure and whether the site was grassland/parkland, garden or woodland.

epiphytic community composition. The measured bark characteristics only explain a small amount of the variation in community composition and had only limited overlap (2–3%) with the variation explained by tree characteristics. This contrasts with results obtained by Jürriado et al. (2009), who found that substrate-specific effects, notably bark pH, were the dominant factor in determining lichen species cover on trees rather than tree species. However, our work does concur with Spier et al. (2010) and Mežaka et al. (2012), who found that tree species was an important factor influencing epiphytic communities.

The results suggest that bark characteristics cannot be used for providing clear guidance on the suitability of substitute phorophytes and raises the question of what are the distinguishing tree characteristics that cause the differences in epiphytic community composition? Spier et al. (2010) suggest that factors such as bark water-holding capacity, bark roughness or other bark chemical properties may be responsible. However, here these variables were included and the “tree characteristics” group of variables still explained more of the variation. Further analysis could explore if tree species or the other variables within the “tree characteristics” group (height, DBH and canopy cover) are most important in explaining the variation. For example, it could be light availability and/or relative humidity influenced by canopy cover or tree size (and hence length of time for colonization to occur) that are important. Other reasons for close relationships between lichens and tree species, which have yet to be explored in depth, include water uptake by the lichens, biophysical attributes such as fungus-specific

surface adhesion and differences between lichens in carbohydrate sourcing (Resl et al. 2018).

It is well known that site characteristics such as pollution (Johnsen & Sørensen, 1974; A.P.R.I.L., 2002) and climate will influence epiphytic composition. Here, site did not explain more of the variation in epiphytic community composition than “tree characteristics,” possibly because our sites were deliberately chosen to be as similar as possible in climate and pollution. However, local pollution and climatic conditions will influence the suitability of phorophytes to replace any given tree species; as lichen colonisation is influenced by pollution levels which influence bark pH (Bates et al. 1990; Bates et al. 1996; Hauck et al. 2011).

4.3 | The role of non-natives?

This work provides evidence of the suitability of non-native oaks and one non-native hybrid, *Tilia × europaea*, for supporting OA and POA epiphytes despite differences in bark characteristics. Thus, some non-natives, particularly those of the same genera, may be suitable substitute phorophytes. However, in some instances non-native trees have been shown to impact on other aspects of biodiversity (e.g., ground flora), and ecosystem functioning (e.g. decomposition and nutrient cycling; Ennos et al. 2019; Mitchell et al. 2021); factors which should be taken into account when considering the establishment of non-natives.

4.4 | Conservation implications

Diversification of tree species composition within forests is recommended to increase resilience against climate change and pests and pathogens (Meason & Mason, 2014; Wilson, 2014). However, this concept is rarely discussed in relation to non-woodland trees, such as primarily studied here, but see Liira et al. (2020) and Kubiak and Osyczka (2019). To provide increased resilience the tree species present should support as large a proportion of the biodiversity associated with the threatened tree species as possible; however, this information is often lacking (Mitchell et al. 2017; Mitchell et al. 2019a). If the key traits determining host suitability could be identified, these could provide a quick assessment of suitability. However, this work suggests that, at least for lichens and bryophytes, while overall there is a correlation between bark characteristics and epiphytic community composition, the association is weak and bark characteristics cannot be used to provide a clear guide to the suitability of substitute phorophytes to host “at-risk” biodiversity. Moreover, the bark characteristics related to OA epiphytes change depending on whether one considers all the OA species or only those preferentially associated with oak. Tree species and size rather than the measured bark characteristics, site or habitat information explained more of the variation in the OA epiphyte community than bark characteristics. Further work is required to identify which phorophyte traits determine host suitability. Until this is known, recording of

species hosted by non-native and/or less frequently assessed phorophytes should be increased, to allow a proper assessment of their suitability and better conservation management advice.

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AUTHOR CONTRIBUTIONS

RJM and RLH conceived the idea, designed the sampling and carried out data analysis, RJM, RLH and JD carried out the fieldwork and JB contributed to labwork. RJM wrote the manuscript and all authors provided comments. All authors gave permission for this work to be published.

DATA AVAILABILITY STATEMENT

The data are available at NERC Environmental Information Data Centre. <https://doi.org/10.5285/f539567f-a8cd-482e-89b8-64a951b52d93>. Mitchell, R.J.; Hewison, R.L.; Beaton, J.; Hagh, R.K.; Robertson, A.H.J.; Main, A.M.; Owen, I.J.; Douglass, J. (2020). Functional and epiphytic biodiversity differences between nine tree species in the UK.

ORCID

Ruth J. Mitchell  <https://orcid.org/0000-0001-8151-2769>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

- Appendix S1.** Description of habitat of surrounding the trees.
- Appendix S2.** Examples and descriptions of bark patterns recorded. Photographs taken by the authors.
- Appendix S3.** Oak associated lichens on the trunks of nine trees species.
- Appendix S4.** Oak associated lichens on the twigs and branches of nine trees species.

Appendix S5. Oak associated bryophytes (as defined by Mitchell et al 2019a&b) on the trunks of nine trees species.

Appendix S6. Similarity of substitute phorophytes in their bark characteristics to a) *Quercus robur* b) *Quercus petraea*.

Appendix S7. Similarity of substitute phorophytes to native oak species in their hosted community composition of oak associated and preferentially oak associated lichens.

Appendix S8. Similarity of substitute phorophytes to a) *Quercus robur* and b) *Quercus petraea* in their hosted community composition of oak associated bryophytes on the trunk.

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