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# The non-native *Quercus rubra* does not substitute the native *Quercus robur* and *Q. petraea* as substrate for epiphytic lichens and bryophytes

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ABSTRACT

Climate change will cause alterations in tree species ranges. Non-native tree species are likely to be increasingly used in production forests, due to their often better adaptation to a warmer climate and their lower susceptibility to pests and pathogens. Trees form an important habitat for numerous species, many of which are more or less specialised regarding tree species. Thus, the tree-associated flora and fauna may be heavily impacted if non-native trees replace native ones. Risk assessments from the introduction of non-native trees must rest on a solid knowledge base, including insights into the potential of such trees to function as biodiversity substitutes, i.e. to host similar biodiversity as closely related native tree species. In a study in temperate Sweden, we inventoried epiphytic lichens and bryophytes on ten random trees in each of 28 stands (14 stands of North American red oak *Quercus rubra* and 14 stands of native oak *Q. robur/petraea*), to compare species richness and composition. Overall, 101 lichen taxa and 35 bryophyte taxa were identified, and we found a generally higher diversity for native oak. The regional species richness (gamma diversity) for both lichens and bryophytes was higher in native oak than in red oak, and the lichen species richness at stand level (alpha diversity) was nearly significantly higher. Lichen composition differed between the two oak species, while there was no difference for bryophytes. More lichens were strongly associated with native oak than red oak, while most bryophyte species were generalists with no specific preference for either oak taxa. Bark structure was an important explanatory variable separating the lichen epiphytes, with species preferring smooth bark largely confined to red oak. In conclusion, our study suggests that substituting native oak with red oak could have adverse consequences for epiphytic lichen populations associated with native oak, resulting in a decline of several species. However, certain lichen and bryophyte species were exclusively found on *Q. rubra*, implying that incorporating a proportion of red oak stands in southern Swedish landscapes may enhance diversity. Further research is needed to explore the overlap between species associated with *Q. rubra* and other deciduous tree species that possess similar smooth bark. Our findings indicate that red oak may not be an appropriate alternative host tree for epiphytic lichens typically found on native oak, while the implications for bryophytes remain less clear.

## 1. Introduction

Climate change poses a considerable pressure on the world's forests, with predicted marked future alterations in the ranges of tree species, also affecting their vast number of associated species (Walther, 2010). In regions with extensive practices of industrial forestry, there may be a need to change tree species if a desired level of wood production is to be maintained. One possibility is to introduce non-native tree species that are better adaptated to warmer climates (Ennos et al., 2019). A further risk from climate change is the rapid expansion of tree pathogens (fungi, insects, microorganisms) which cause damage and death to native trees (Ramsfield et al., 2016). This is another reason to consider a shift to non-native tree species that are less susceptible. Because species that live on and in trees commonly prefer specific tree species (Sundberg et al., 2019; Hämäläinen et al., 2023), a change in tree species composition may have profound consequences for the associated biodiversity.

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Several non-native tree species are controlled in Europe since they are invasive, putting substantial pressure on biodiversity and the function, structure and dynamics of forest ecosystems (Forest Europe, 2020). A thorough understanding of biodiversity responses is vital for making sound decisions regarding the rules and regulations for introduction and management of non-native tree species.

Non-native trees were introduced to Europe in the 15th century, and today, nearly 150 species of foreign origin occur in European forests (Pötzelsberger et al., 2020). The share of non-native tree species of all tree species is low, e.g. only 3% in Europe's forests, but increasing (Forest Europe, 2020). However, in forest plantations (intensively managed planted forests with one or two tree species, even age-class and regular spacing; FAO, 2020), non-native tree species comprise on average >50% of the tree species in Europe, with a similar fraction globally (Forest Europe, 2020, FAO and UNEP, 2020). The biodiversity response to the introduction of non-native tree species is highly variable and seems to strongly depend on study system and study design. For example, Quine and Humphrey (2010) compared non-native and native tree species in the UK, and found positive, negative or neutral results depending on tree species, region and taxonomic group. Effects from non-native trees on ecosystem services also seem context-dependent, and to vary greatly depending on tree species, biome and socio-economic conditions (Castro-Díez et al., 2019).

In a world where tree species distributions are changing, and where the fundamental goal of biodiversity conservation is to maintain native flora and fauna, one option could be to introduce non-native tree species. These could serve as substitute tree species if they support a biodiversity similar to that of native tree species (Ennos et al., 2019). Such substitute tree species could be most successful if they are phylogenetically similar to the native tree species (Kärvemo et al., 2023). Epiphytes, i.e. plants that grow on trees, are often associated with specific tree species, driven by variation of tree traits such as architecture, bark structure, bark and leaf chemistry, affecting microclimate, nutrient composition and stability (Ellis, 2012). Diversity in microhabitats on trees increases the number of available niches and promotes species richness of numerous taxonomic groups, including bryophytes and lichens (Larrieu et al., 2018). Lichens and bryophytes are commonly used as model organisms in studies on drivers of forest biodiversity, and also as biodiversity indicators, due to their large habitat specificity and high species number (Ellis, 2012; Czerepko et al., 2021).

One appropriate study system to test the concept of substitute tree species is epiphytic bryophytes and lichens on native and non-native oaks *Quercus*, a tree genus belonging to the family Fabaceae with about 500 species in the Northern Hemisphere (Russell et al., 2020). *Quercus robur* and *Q. petraea* are two closely related, indigenous species of temperate Europe (in the following treated as one taxon, named *Q. robur/petraea*, "native oak") while *Quercus rubra* red oak is native to North America. All three species belong to subgenus Quercus while *Q. robur* and *Q. petraea* belong to section Quercus and *Q. rubra* to section Lobatae (Zhou et al., 2022). Section Quercus is characterised by rounded leaf tips, wheareas section Lobatae has sharp tips. The bark structure of native oak is fissured, while it is relatively smooth in red oak (Fig. 1). *Q. robur/petraea* are at risk of decreasing in Europe due to attacks by insects and fungi (e.g. Denman et al., 2014; Lonsdale, 2015; Tomlinson et al., 2015). *Q. rubra* has been used as a wood production tree and for its ornamental value in Europe since the 18th century (Dyderski et al., 2020). Due to its high growth rate, pathogen resistance and drought tolerance, it is, from a climate change perspective, considered an alternative to native trees in production forestry (Dyderski et al., 2020; Fahlvik and Johansson, 2021). However, our understanding of how introducing red oak may affect forest biodiversity is limited (Wohlgemuth et al., 2022), leaving us uncertain if red oak could serve as a biodiversity substitute for native oak.

The main aim of this study is to enhance our understanding of biodiversity response from the introduction of non-native tree species. We do this in the framework of substitute tree species, and compare epiphytic bryophytes and lichens on the native oak *Q. robur/petraea* and the non-native red oak *Q. rubra*. Our study region comprises the southernmost part of Sweden, a northern outpost of the European temperate forest belt (Ahti et al., 1968), and the core area of oak in the country. We are interested in the role of red oak as a possible replacement for native oak, and want to explore biodiversity associated with the different oak species, such as species number, composition and complementary.

We aim to test the following hypotheses:

- the number of epiphytic bryophyte and lichen species will be higher on native oak than on non-native red oak, and species composition will differ between the two oak taxa
- this pattern will be evident at alpha (stand), beta (among stand) as well gamma (regional) level

**Fig. 1.** The bark structure, a key determinant of epiphyte composition, is fissured in the native oak *Quercus robur/petraea* (left) while it is smooth in the non-native red oak *Q. rubra* (right). Photo: Victor Johansson.

## 2. Material and methods

### 2.1. Selection of stands

The study was conducted in southern Sweden (midpoint N 56°16′, E 13°41′) in the counties of Halland, Skåne, and Kronoberg, covering a total area of 7 200 km$^2$ (Appendix Fig. A.1.). Oak stands managed for forest production were selected, i.e., stands that had been managed through thinnings, leading to more or less evenly spread trees with straight stems.

Potential stands (about 60) were identified from the database Silvaboreal (compilation of forest research sites www.silvaboreal.com), the database of the Swedish Forest Agency on seed-selection forests, sites used in earlier studies (Jörning, 2019; Fahlvik and Johansson, 2021), and through personal contacts with landowners. Based on field visits, 14 stands of red oak and 14 stands of native oak were selected (Appendix Fig. A.2.), fulfilling set-up criteria of: >0.1 ha in size, >80% of tree stems >10 cm in diameter at breast height of the target tree taxa, predominantly flat terrain, age >50–100 years, and with signs of forest management measures, i.e. indications that they were forest production stands. Information on stand ages was retrieved from the databases and forest registers of authorities and forest owners (Jörning, 2019, Fahlvik and Johansson, 2021). The final selection was made with the additional criterion of a minimum distance to another stand of 700 m.

### 2.2. Selection of trees and recording of epiphytes

In every stand, five randomly selected points were marked on a digital map, with the criteria of >10 m distance from each other and >5 m from stand edge other than forest (road, clearcut, watercourse, agricultural land etc.). At every point, two sample trees >10 cm in diameter at breast height (1.3 m) were randomly chosen, amounting to 10 trees per stand. The first sample tree was the one closest to the random point, the second was >5 m from the first one in the direction N-NE (90° segment), and if none was present in this segment within a 20 m distance, the search continued successively in a clockwise manner, in 90° segments. On each sample tree, presence of all species of lichens and bryophytes from the ground up to 2 m height was recorded. Cover of bryophytes was registered with a caliper in the same area, in 10% intervals (0–10, 11–20…91–100%). The diameter at breast height was measured for each sample tree and depth of bark crevices in the four cardinal directions, N, S, E, and W, using a metal ruler (Johansson et al., 2009). At each of the 5 randomly selected points per stand, the basal area of trees, separated into tree species, was estimated through relascope measurement. Nomenclature follows the Swedish taxonomic database (Dyntaxa; https://www.dyntaxa.se).

### 2.3. Statistical analysis

All statistical analyses were executed using the R software, version 4.2.2 (R Core Team, 2023). To illustrate the number of unique and shared lichen and bryophyte taxa for native oak and red oak, we used a Venn diagram. To compare species richness across all stands between native oak and red oak (gamma diversity) we also constructed species accumulation curves for lichens and bryophytes separately, with 1000 permutations and sites added in random order (function specaccum in R package vegan, Oksanen et al., 2013). Statistical interpretation can be made by comparing the confidence bands around the curves (Gotelli and Colwell, 2001). To test the difference in the number of lichen and bryophyte taxa (separately) per stand between native oak and non-native red oak (tree taxa as an explanatory variable), we used generalized linear models with Poisson distributions (R package glmmTMB, Brooks et al., 2017). To evaluate the contribution of different environmental variables, we then tested the explanatory power of stand age, bark depth, tree diameter, basal area, bryophyte cover, longitude and latitude for native oak and red oak stands separately (one model for each oak species) using the same type of model. For models of bryophyte richness, we did not include bryophyte cover as explanatory variable. Model selection was based on AIC and the final ‘best’ model had the lowest AIC.

To compare the lichen and bryophyte dissimilarity among stands (beta diversity) between native oak and red oak we used two different similarity indices (Sorenson and Bray-Curtis) obtained with the betapart package in R (Beselga and Orme, 2020). The Sorensen index only considers species occurrence (presence/absence) while the Bray-Curtis index also accounts for species abundance (here the number of occupied trees). Differences in the pairwise lichen and bryophyte dissimilarity among stands of each tree taxa was assessed with a separate ANOVA for each of the two indices.

A nonmetric multidimensional scaling (NMDS) analysis was performed on a species by site matrix to describe the stand level species composition of lichen and bryophytes. The NMDS was performed with the metaMDS function in the R package vegan (Oksanen et al., 2013) using the Bray–Curtis dissimilarity measure and default settings. Significant relationships between species composition and the explanatory variables were assessed with Permutational Multivariate Analysis of Variance (PERMANOVA, function adonis2 in R package vegan). We investigated the marginal effect of the variables (instead of the default sequentially test of terms, which is sensitive to the order of added variables). First, we tested the difference between the two oak species for lichens and bryophytes separately (i.e., one model for each species group). Then we tested the explanatory power of the environmental variables, and longitude/latitude, for native oak and red oak stands separately. For the analysis of bryophyte composition, we did not include bryophyte cover as an explanatory variable.

To reveal the lichen and bryophyte species that contributed most to the differences in species composition between stands of the two tree taxa, we also performed an indicator species analysis for both species groups (Dufrêne and Legendre, 1997) using the ‘indval’ function in the R package labdsv (Roberts, 2016).

## 3. Results

### 3.1. Species richness

The total species richness over the whole study region (28 study stands and 280 trees; gamma diversity) was 101 for lichens and 35 for bryophytes (Fig. 2 and Appendix Table A.1.). The most common lichen taxa were *Lepraria* sp. (found on 277 trees), *Cladonia coniocraea* (260), *Micarea prasina* s.l. (229), *Phlyctis argena* (203), and *Biatora efflorescens* (191). The most common bryophyte taxa were *Hypnum cupressiforme* (found on 277 trees), *Dicranum scoparium* (152), and *Dicranum montanum* (122). Native oak harboured 92 lichen taxa and 31 bryophyte taxa in total, and the corresponding numbers for red oak were 67 and 27. Native oak had 34 unique lichen taxa (only found on this tree taxon) and eight bryophyte taxa, while only nine lichen taxa and four bryophyte taxa were unique for red oak (Fig. 2).

On average, 28.9 lichen taxa and 8.6 bryophyte taxa were found in stands of native oak, and the corresponding numbers for red oak were 25.1 and 7.6, with no significant difference between the two oak species (Fig. 3), even if there was a tendency for lichens ($p = 0.054$).

The total number of lichen species over the study area (gamma diversity) was significantly higher for native oak with an estimated 106 species compared to 76 species for red oak based on the non-overlapping confidence intervals of the species accumulation curves (Appendix Fig. A.2.). The difference for bryophytes was smaller with an estimated 36 species for native oak and 31 for red oak.

For native oak, the number of lichen taxa increased with increasing tree diameter and decreased with increasing basal area, bryophyte cover and latitude (Table 1; see Appendix Fig. A.3. for environmental variables). The number of bryophyte taxa increased with latitude. For red oak, the number of lichens was not associated with any of the

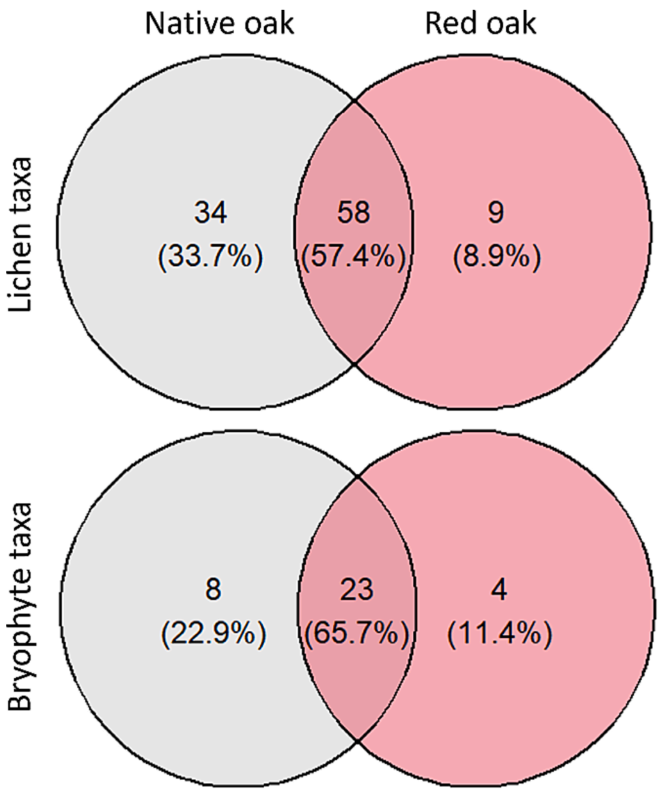

**Fig. 2.** Venn diagram dividing the regional γ-diversity into unique and shared lichen and bryophyte taxa for native oak and red oak.

explanatory variables, while the number of bryophyte taxa increased with increasing stand age (Table 1).

### 3.2. Species composition

The stand dissimilarity in species composition for lichens was larger for native oak than for red oak both according to the Sorensen index ($F = 9.17$, $p = 0.005$) and the Bray-Curtis index ($F = 5.02$, $p = 0.034$) (Fig. 4), while there was no difference for bryophytes.

There was a clear difference in the species composition for lichens ($R^2 = 0.22$, $F = 7.19$, $p = 0.001$) between the two tree taxa, while there was no difference for bryophytes ($R^2 = 0.04$, $F = 1.15$, $p = 0.32$), Fig. 5. The species composition of lichens within native oak stands was explained by bark fissure depth, basal area, bryophyte cover and latitude, while only bark fissure depth explained the lichen composition among red oak stands (Table 2). The composition of bryophytes was explained by latitude in native oak stands, while none of the variables explained the composition in red oak stands.

Eight lichen taxa and one bryophyte species were indicators for native oak, and seven lichen taxa and no bryophyte were indicators of red oak. Table 3.

## 4. Discussion

Native oak harboured more lichen species in total and showed a larger species variation among stands than red oak. This and the clear difference in overall species composition between the two oak taxa is consistent with our hypotheses. In contrast, bryophytes showed less clear differences in species numbers and composition. Red oak is, thus, an unsuitable substitute host tree for lichens, while the results for bryophytes are more inconclusive.

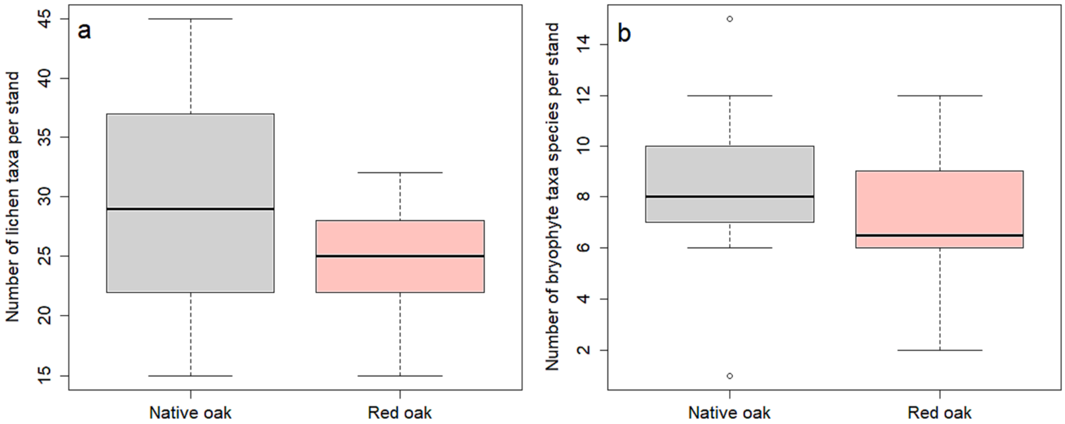

**Fig. 3.** Species richness per stand (α-diversity) for (a) lichen and (b) bryophyte species associated with native oak and red oak.

**Table 1**
Parameter estimates (with SE) from generalised linear models of the number of lichen and bryophyte taxa on native oak and red oak as a function of tree diameter, basal area, bryophyte cover, stand age, and latitude. ΔAIC = change in AIC when removing the variable from the final model. Only variables improving model fit are presented.

| | Native oak | | | | Red oak | | | |
|---|---|---|---|---|---|---|---|---|
| | Lichens | | Bryophytes | | Lichens | | Bryophytes | |
| Explanatory variable | Est | ΔAIC | Est | ΔAIC | Est | ΔAIC | Est | ΔAIC |
| Tree diameter | 0.15 (0.06) | 4.3 | | | | | | |
| Basal area | −0.11 (0.07) | 0.4 | | | | | | |
| Bryophyte cover | −0.18 (0.07) | 6.0 | | | | | | |
| Stand age | | | | | | | 0.22 (0.10) | 2.9 |
| Y-coordinate (latitude) | −0.10 (0.06) | 1.6 | 0.31 (0.10) | 8.1 | | | | |

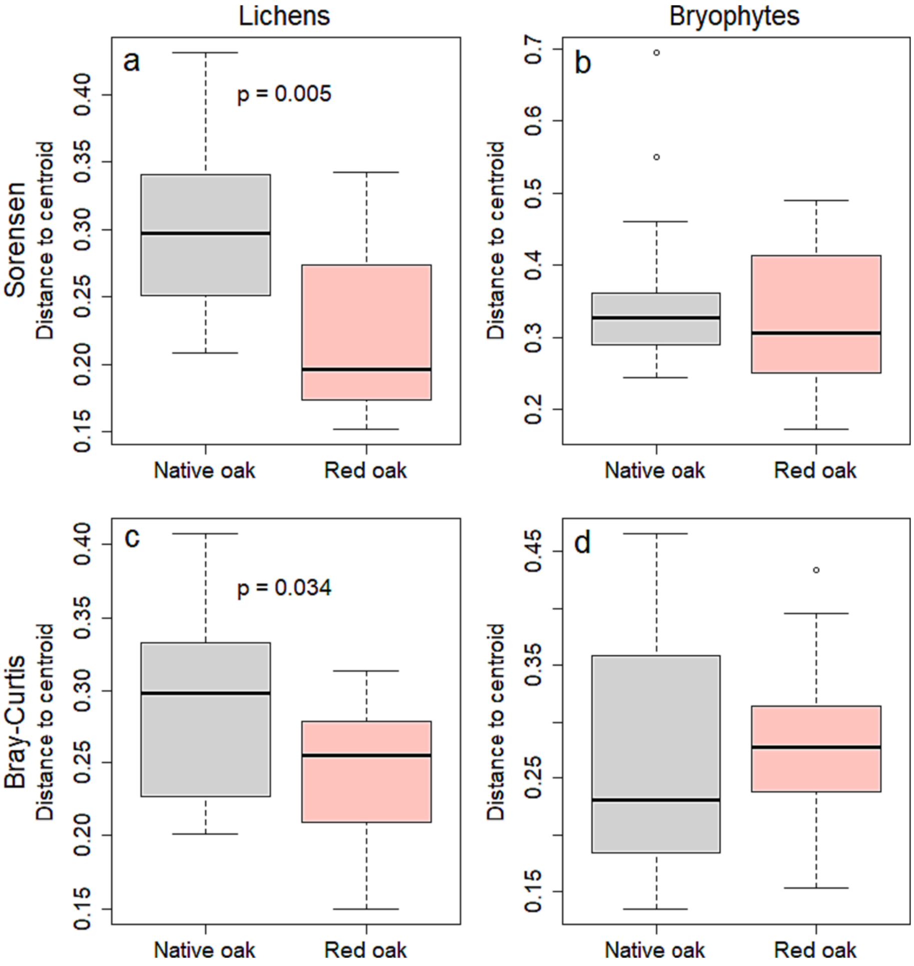

**Fig. 4.** The dissimilarity between stands (β-diversity) of lichens (a, c) and bryophytes (b, d) according to the Sorensen index (a, b) and the Bray-Curtis dissimilarity index (c, d).

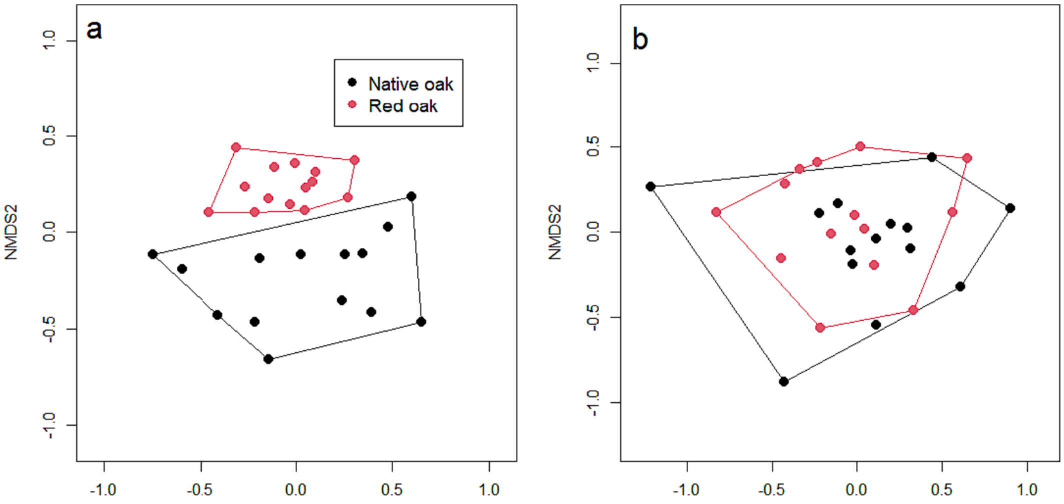

**Fig. 5.** The composition of (a) lichen (stress = 0.18) and (b) bryophyte (stress = 0.19) taxa among stands of native oak and red oak.

### 4.1. *Species richness*

We show that there were more lichen species in total (higher gamma diversity) on native oak compared to red oak, and a tendency for the same pattern was also seen for the stand-level species richness (alpha diversity). Of all recorded lichen species, more than a third (34%) were found exclusively on native oak, compared with 9% for red oak, indicating a clear preference for native oak. For instance, *Arthonia vinosa* and *Biatora globulosa* were recorded on 48 and 12 native oak trees, respectively, with no recording on red oak. Almost all of the nine lichen species unique to red oak were singletons, i.e. found on one tree only. There were also species in common between the two tree taxa but with a clear

**Table 2**
The $R^2$ and associated level of statistical significance for the explanatory variables in Permutational Multivariate Analysis of Variance of the lichen and bryophyte compositions among stands of native oak and red oak.

| | Native oak | | Red oak | |
|---|---|---|---|---|
| Explanatory variable | Lichen | Bryophyte | Lichen | Bryophyte |
| Bark depth | $R^2 = 0.16^{***}$ | | $R^2 = 0.23^{***}$ | |
| Basal area | $R^2 = 0.13^{**}$ | | | |
| Bryophyte cover | $R^2 = 0.09^{*}$ | | | |
| Y-coordinate (latitude) | $R^2 = 0.18^{***}$ | $R^2 = 0.28^{**}$ | | |

**Table 3**
Lichen (L) and bryophyte (B) taxa associated with native oak and red oak with indicator value and the corresponding p-values.

| **Species** | **Indicator value** | **p-value** | **Tree** |
|---|---|---|---|
| *Anisomeridium biforme* (L) | 0.36 | 0.036 | Native oak |
| *Arthonia spadicea* (L) | 0.84 | 0.001 | Native oak |
| *Arthonia vinosa* (L) | 0.79 | 0.001 | Native oak |
| *Biatora globulosa* (L) | 0.36 | 0.041 | Native oak |
| *Cladonia coniocraea* (L) | 0.52 | 0.035 | Native oak |
| *Coenogonium pineti* (L) | 0.61 | 0.034 | Native oak |
| *Lecanactis abietina* (L) | 0.41 | 0.028 | Native oak |
| *Pertusaria pertusa* (L) | 0.40 | 0.037 | Native oak |
| *Plagiomnium affine* (B) | 0.36 | 0.040 | Native oak |
| *Buellia griseovirens* (L) | 0.78 | 0.001 | Red oak |
| *Fuscidea cyathoides* var. *Corticola* (L) | 0.50 | 0.011 | Red oak |
| *Fuscidea pusilla/F. arboricola/Ropalospora viridis* (L) | 0.71 | 0.002 | Red oak |
| *Graphis scripta* (L) | 0.57 | 0.001 | Red oak |
| *Parmeliopsis ambigua* (L) | 0.65 | 0.021 | Red oak |
| *Scoliciosporum chlorococcum* (L) | 0.71 | 0.002 | Red oak |
| *Violella fucata* (L) | 0.84 | 0.001 | Red oak |

preference for one or the other, as shown in the indicator species analysis. Interestingly, most of the epiphyte species preferring red oak are otherwise, in southern Sweden, found on broadleaved tree species with smooth bark, such as *Betula* spp., *Corylus avellana, Fagus sylvatica* and *Sorbus aucuparia* (Thor, 2020), demonstrating the importance of bark type as a microhabitat. One example is *Fuscidea cyathoides* var. *corticola* that was found on 39 red oak trees but on no native oak tree, and others include *Buellia griseovirens* and *Graphis scripta*.

The similar bryophyte species richness between the two oak taxa at the stand (alpha) level is probably due to most of the species being rather common generalists, frequently occurring as epiphytes on broadleaved trees in temperate Sweden (Hallingbäck, 2016). The only bryophyte species with a marked difference between the two oak taxa was *Plagomnium affine*, found on ten native oak trees and on no red oak tree. This species is common in southern Sweden with a wide habitat-amplitude, occurring in forests as well as on agricultural land (Hallingbäck, 2016). It is associated with a rather high humidity and grows on tree-bases and more rarely higher up on stems. The more varied structure and likely also water-holding capacity of the bark of native oak seem to provide better growing conditions than the smoother bark of red oak. Other unique bryophyte species (seven for native oak and four for red oak) occurred on very few trees, making interpretations difficult.

Our results with deviating responses of lichens and bryophytes agree with a recent analysis of epiphyte tree hosts in the UK (Mitchell et al., 2021a), revealing a higher lichen than bryophyte specificity for native oak. They found that 30% of the lichen species on native oak only occurred on this tree species or preferred it over other tree species while all epiphytic bryophytes associated with native oak also occurred on a wide range of other tree species. Woziwoda et al. (2017) also found a high similarity of epiphytic bryophytes between *Q. robur/petraea* and *Q. rubra.*

Comparable empirical investigations on epiphytes involving the two tree taxa at a large geographical scale, the gamma level, are scarce, varying largely in methodology and studies including both bryophytes and lichens are lacking. In our study area of about 7 600 km$^2$ we surveyed 140 trees of red oak and native oak, respectively, and found approximately 90 lichen and 30 bryophyte species for native oak and 70 and 30 for red oak. To illustrate the difficulty in contrasting results, Stubbs (1989), in an area of appr. 70 km$^2$ in Maine, i.e. within the natural range of red oak, found 39 lichen species on 32 red oak trees, but without comparing with other tree species. Kubiak (2006) reported 59 lichen species on an unknown number of red oak trees from an area likely 500 km$^2$ in size in Poland. Woziwoda et al. (2017), also in Poland, found 28 epiphytic bryophyte species on red oak and 22 on native oak with many trees investigated, in a study embracing 170 km$^2$.

### 4.2. *Species composition*

The species composition, as species richness, clearly differed between the two oak taxa for lichens but not for bryophytes. The separation in lichen communities is in line with a review of a number of taxonomic groups associated with native oak in relation to other tree hosts in the UK by Mitchell et al. (2019). Within native oak and red oak, respectively, depth of bark fissures was an important variable explaining the lichen (but not the bryophyte) composition. The smooth bark of *Q. rubra* contrasts with the more marked fissure structure of native oak (Fig. 1), but still there evidently was a small signal for fissure depth within this tree species. Bark properties are known to be important for epiphytic lichens in general (Barkman, 1969), and shown for several species specialised on native oak (Johansson et al., 2010), so this result was not surprising. Still, our results contrasts with a study by Mitchell et al. (2021a) in which bark traits were less important than other tree characteristics (tree species, height, diameter at breast height and canopy cover) for bryophytes and lichens associated with *Q. robur/petraea* and potential substitute host tree species. One explanation to our diverging results may be that Mitchell et al. (2021a) analysed <35 trees of each tree species, possibly capturing only a limited bark variation. Tree age, which commonly is a driver of epiphytic species (Fritz et al., 2009; Lie et al., 2009) was not significant for the composition of either lichens or bryophytes. This may be due to the relatively short time-span in ages of the studied stands.

### 4.3. *Red oak as a substitute host tree*

Dyderski et al. (2020) in an overview of various ecological aspects of *Quercus rubra* concluded that negative biodiversity impacts are prevailing when planted in Europe. For instance, abundance and diversity in the ground vegetation decreases (Chmura, 2013; Woziwoda et al., 2014), likely from the deep shade of the canopy and the thick litter layer (Dobrylovská, 2001). In comparison with native oak, microbial biomass in the soil is lower (Stanek and Stefanowicz, 2019), there is a negative impact on soil fauna (Gentili et al., 2019) and the reproductive ability of the tree is considerably higher, with a risk of invasiveness (Woziwoda et al., 2019). In contrast, other studies have revealed that red oak can host a rich biodiversity outside its natural distribution area. For instance, Vogel et al. (2021), in a recent study in Germany, found red oak to host the third highest number of saproxylic beetles at alpha level and also a comparatively high number of red-listed species, of 47 investigated native and non-native tree species. In our study, we found only two red-listed species (both lichens) and only on native oak:

*Bactrospora corticola* (one tree) and *Opegrapha vermicellifera* (two trees) indicating that a much larger sample than ours is needed to capture the rarest species. Woziwoda et al. (2017) surveyed epiphytic bryophytes in Poland and concluded that red oak indeed can act as a substitute to native oaks since they found large number of species, including uncommon ones. Mitchell et al. (2019) in their study on oak-associated species in the UK found that other tree species share maximum 40% species with oak. In a related study Mitchell et al. (2021b) showed that non-native oak species could only replace native oak for a few of functions and ecosystem services that they measured. Thus, should there be an accelerating decline in native oak, there is no good substitute tree species.

### 4.4. Conclusions

Our study expands the knowledge on the biodiversity associated with the North American red oak in Europe, and our comparisons with the native native oak increase insights further. If red oak was to replace native oak large-scale in southern Sweden, our results suggest negative consequences for epiphytic lichens, with a potential decrease of many species. Thus, for this taxonomic group, red oak is not a substitute for native oak. In contrast, the impact on common bryophytes would most likely be small. Still, some lichen as well as bryophyte species were found on red oak only, pointing to some degree of complementarity with native oak. Thus, adding a certain share of red oak stands to south forest landscapes could increase diversity. Nevertheless, in order to make such landscape-scale evaluations, further studies are needed on the degree of overlap between species associated with red oak and other deciduous tree species with a similar, smooth bark, such as beech, birch, hazel and rowan. For general conclusions regarding biodiversity effects of non-native tree species, knowledge on many taxonomic groups is an advantage.

## Author contributions

Lena Gustafsson participated in the design of the study, selected fields study sites, designed field methods, instructed field workers, and wrote most of the manuscript.

Markus Franzén participated in the design of the study and in the selection of field study sites, took part in field work and participated in manuscript writing.

Johanna Sunde participated in the design of the study, advised on the statistical analyses and took part in the writing of the manuscript.

Victor Johansson participated in the design of the study and in the selection of field study sites, performed the statistical analyses and took substantial part in the writing of the manuscript.

## Declaration of Competing Interest

None.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121482.

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