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ORIGINAL PAPER

Biodiversity impacts of native versus non-native oaks

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Abstract Introducing non-native tree species into forest ecosystems is a growing trend, in part as climate change may cause a decline of native species and shifts in species distributions. In European forestry, *Quercus rubra* (northern red oak) has increasingly been considered a candidate substitute species for native oaks. However, it remains largely unknown how this substitution affects associated biodiversity. This study compares the biodiversity supported by the native oak species *Q. petraea* (sessile oak) and *Q. robur* (pedunculate oak) and the invasive *Q. rubra* in southern Sweden, focusing on both oak-associated organisms and general forest biodiversity. Arthropods were sampled using Malaise traps at the site level. At the same time, vascular plants, leaf herbivory and endophytic insects (leaf miners and gallers) were recorded at the tree level in three sites per oak species. Our results reveal guild-specific effects of oak species on biodiversity. The introduced *Q. rubra* supported significantly fewer endophytic insects than native oak species. Vascular plant species richness was marginally lower in *Q. petraea* and *Q. rubra* sites compared to *Q. robur*. In contrast, the species richness, abundance, biomass and community composition of arthropods and leaf herbivory did not differ significantly between the three oak species. These findings indicate that the ecological consequences for biodiversity of introduced tree species, such as *Q. rubra*, are most pronounced for specialised herbivores, including leaf miners and gallers, and suggest

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that broader forest biodiversity measures may be less responsive to changes in tree species than to local environmental conditions.

Keywords Biological diversity · Forest management · Invasive species · Leaf herbivory · *Quercus* · Non-native species · Vascular plants

Introduction

Global warming, pest outbreaks, and the deliberate or unintentional introduction of non-native species, combined with intensive forestry practices and agricultural expansion, exert increasing pressure on the forests of the world (Forzieri et al. 2022). Non-native forest trees and invasive pests are among the primary drivers of forest transformation, altering species composition, structure, and function at unprecedented rates (Liebhold 2012). Climate change amplifies these impacts through two key mechanisms: increasing mortality in economically important species such as spruce (Felton et al. 2020) and driving substantial shifts in tree species distributions, with populations moving poleward and upward in elevation to track suitable climatic conditions (Hamann & Wang 2006; Hartmann et al. 2022). Projections indicate that ongoing changes in tree species distribution, abundance, and age structure throughout the twenty-first century will significantly affect the biodiversity of organisms reliant on forest habitats (Pureswaran et al. 2018). The combined pressures of invasive species, climate change, and human activities accelerate forest degradation, highlighting the urgent need for management strategies that integrate biodiversity conservation with sustainable forestry practices (Xu et al. 2023).

In regions dominated by intense forestry, there is a growing interest in introducing non-native tree species that are better adapted to the emerging conditions as they may be predisposed to cope with higher temperatures, modified precipitation regimes, more extreme weather conditions, and more frequent and severe outbreaks of both native and invasive pests and pathogens (Ennos et al. 2019; Pötzelsberger et al. 2020). For example, non-native trees, such as *Quercus rubra* L. (northern red oak), have been introduced into European forests since the eighteenth century, primarily for timber production and ornamental purposes (Májeková et al. 2024; Merceron et al. 2017). As climate change accelerates the decline of some native tree species, *Q. rubra* is more often considered a viable alternative in production forestry due to its rapid growth, drought tolerance, and resistance to pathogens (Chmura 2020; Gebeyehu & Hirpo 2019). However, the introduction of non-native tree species can have profound and complex consequences for biodiversity, especially in ecosystems where the native trees play a critical role in supporting a wide range of species (Gustafsson et al. 2023; Hämäläinen et al. 2023; Post et al. 2009; Tyler et al. 2015). Substituting native oak species, such as *Q. petraea* (Matt.) Liebl. (sessile oak) and *Q. robur* L. (pedunculate oak), with *Q. rubra*, has been shown to modify soil physicochemical properties and forest understory vegetation (Stanek et al. 2020). *Quercus rubra* accelerates litter decomposition, lowers soil pH and increases base-cation leaching, thereby favouring nitrophilous herbs and hindering calcicolous species (Woziwoda et al. 2014) and lichen diversity (Gustafsson et al. 2023). Given the keystone role of oaks, the ecological implications of substituting this type of oak species are potentially far-reaching. Yet, the consequences for many dimensions of biodiversity and forest health remain to be investigated (Dyderski et al. 2020; Laux et al. 2022).

Besides providing insights into the responses of hitherto understudied taxa, additional comparative studies are needed to assess the reproducibility of research findings and identify context-specific responses (Voelkl et al. 2020). Understanding the ecological consequences of oak species substitution necessitates investigation across multiple spatial scales, ranging from individual trees to forest sites. Key areas for further research include the impacts on vascular plants (Avon et al. 2010) and arthropods, particularly herbivorous insects (Southwood et al. 2005). The variation in herbivorous insect abundance and diversity patterns among different oak species is particularly relevant for forest management and conservation, as these interactions play a fundamental role in tree growth, survival, and ecosystem processes (Kozlov et al. 2015; Pearse & Hipp 2009). Of special interest are also the endophytic insects, leaf miners and gallers, that generally are adapted to and target a single or few closely related host species (i.e. specialist species) (Ekholm et al. 2019; Tooker & Giron 2020). It remains to be determined whether *Q. rubra* supports fewer specialist species in line

with the enemy release hypothesis, which posits that herbivores in the introduced range are less likely to utilise novel host species (Keane & Crawley 2002). Recent cross-Atlantic findings indicate that exotic trees indeed often host fewer herbivores overall yet may remain susceptible to generalist insects (Berthelot et al. 2023).

Studies have shown that *Q. petraea* and *Q. robur* both support high levels of biodiversity compared to other tree species, such as pine and spruce, in temperate European forests, particularly in terms of associated arthropods and endophytic insects (Southwood 1961). Native oaks typically sustain higher local richness of epiphytic lichens, saproxylic beetles and Lepidoptera than co-occurring conifers such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Southwood et al. 2004). Both species are considered ecological keystones, providing critical habitat and resources for numerous organisms (Mitchell et al. 2019; Thunes et al. 2021). While sharing many ecological functions, these native oaks have evolved distinct physiological adaptations that influence their growth and survival under different environmental conditions such as soil type, moisture availability, and nutrient status (Eaton et al. 2016). *Quercus petraea* is physiologically tolerant of drought, low pH (≤ 4.5) and shallow soils, whereas *Q. robur* requires mesic, base-rich substrates and is less frost-resistant (Eaton et al. 2016; Ellenberg et al. 1991). Understanding these species-specific characteristics and their associated biodiversity patterns is important for predicting how the substitution of native oaks with non-native species might affect forest ecosystems.

In the present study, we investigated biodiversity patterns at two hierarchical scales, tree- and site-level, across two native oak species (*Q. petraea* and *Q. robur*) and the introduced *Q. rubra* in southern Sweden. At the tree and site level, we focused on leaf herbivory, endophytic insects, and vascular plants, examining whether and how the degree of herbivory, species richness, and community composition differ according to oak species. At the site level, in addition to the estimates above, we also assessed species richness, abundance, community composition, and biomass of arthropods using catches from Malaise traps to capture the forest-level biodiversity associated with the different oak species. We hypothesised that native oaks support greater biodiversity than *Q. rubra*, which is expected to host a distinct, less diverse species assemblage. Furthermore, we compared biodiversity between the native oak sites, hypothesising that *Q. petraea*, which thrives and are adapted to warmer, more acidic, and harsher environments (Eaton et al. 2016), might host different communities of vascular plants and arthropods compared to the more nutrient-rich habitats typically associated with *Q. robur* (Ellenberg et al. 1991). By examining biodiversity at these hierarchical scales, this study aims to provide insights into the ecological impacts of oak species substitution on forest ecosystems.

Methods

Study area and site selection

The study was conducted in southern Sweden across three counties: Halland, Skåne, and Kronoberg (Fig. 1a, b). The sites occur within the same boreonemoral vegetation zone, sharing similar forest structure (oak-dominated deciduous stands) and climate, despite being 200 km apart. The land use history of this region encompasses centuries of traditional management, with much of the original deciduous forest now converted into production forests dominated by spruce and pine.

To minimise the confounding effects of environmental variation, we selected study sites where these species grow under similar climate conditions, allowing us to focus on the effects of tree species rather than underlying geographical differences in species composition. We selected nine forest sites, ranging from 1.3 to 3 hectares, with three sites for each of the three oak species (*Q. robur, Q. petraea* (Fig. 1f), and *Q. rubra* (Fig. 1g), where each oak species was the dominant tree species in its stand. The dominant tree species were defined as those contributing $\geq 50\%$ of the cumulative basal area surrounding seven focal trees. To account for potential confounding effects of tree age, sites were selected to represent a range of tree sizes. For each oak species, this included one site dominated by smaller-diameter trees (mean site DBH 17–25 cm) and two sites with medium- to large-diameter trees (mean site DBH 27–51 cm).

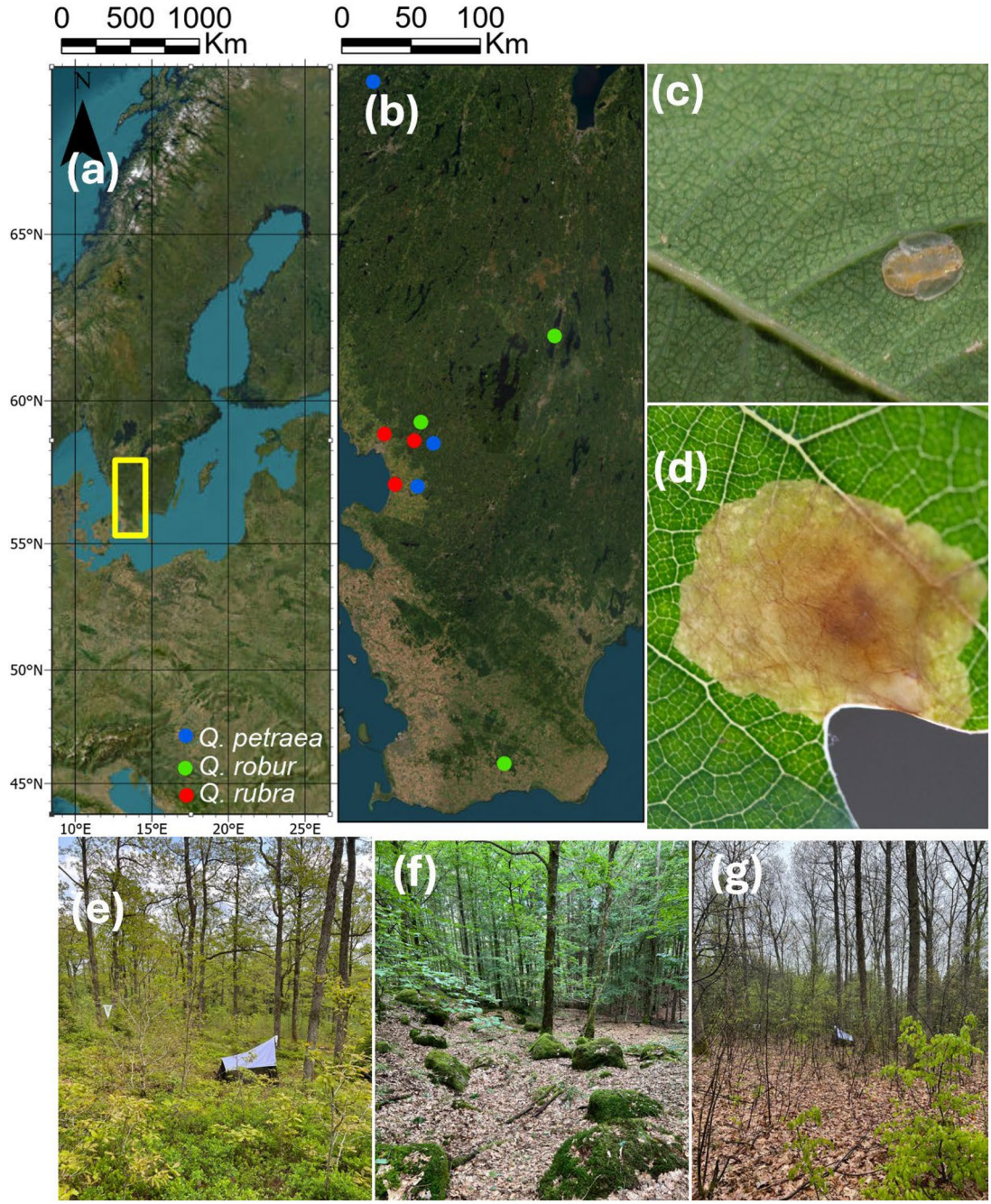

Fig. 1 Geographic distribution of oak forest study sites in southern Sweden. Biodiversity assessments were conducted at both stand level and individual tree level (n = seven trees per site). **a** Study region (yellow rectangle) within Sweden. **b** Distribution of sampling locations for *Quercus petraea* (blue circles), *Q. robur* (green circles), and *Q. rubra* (red circles). **c** *Trioza remota*, psyllid larvae that create galls characterised by a small, raised, and discoloured area on the leaf surface. **d** *Tischeria ekebladella* leaf mine: a characteristic blotch mine created by the larva of the oak-feeding moth *T. ekebladella*, showing extensive internal feeding damage and discolouration of the leaf tissue. **e** Malaise trap deployment in *Q. robur* stand in Bellinga (55.52433°N, 13.68036°E), **f** *Q. petraea* forest at Isakull (56.68295°N, 13.10518°E), and **g** *Q. rubra* at Övraby (56.71575°N, 12.90478°E). Photographs: Ayco Tack (c, d), Markus Franzén (e, f, g)

Data collection

Collection of leaves for herbivory and endophytic insect assessment

To assess whether and how the oak species differed in the amount of herbivory and the species richness of leaf miners and gallers, in late summer 2022 (August one to ten), we sampled sun-exposed branches (2 per tree, opposite sides) using a throw-line launcher, as the forest structure precluded systematic directional sampling (Youngentob et al. 2016). From these branches, we collected the nearest 15 leaves from each branch. Due to a slight variance in the number of leaves collected from each tree (minimum 27), we randomly selected 27 leaves for each tree for the subsequent analyses. After collection, the leaves were dried at 40 °C for 48 h to preserve leaf structure and facilitate storage.

Herbivory

We estimated the leaf area removed following Johnson et al. (2016), which provides a standardised herbivory metric but excludes skeletonisation damage. For each tree, we assessed leaf herbivory by visually estimating the percentage of leaf area removed by chewing insects on individual leaves ($n = 27$ leaves per tree) to the nearest 1%. These percentages were averaged at the tree level ($n =$ seven trees per site) and then at the site level ($n =$ three sites per oak species) for site-level analyses.

Endophytic insects

To assess the species richness of leaf miners and gallers, we scored the presence or absence of each mine and gall taxon on 27 leaves per tree (Fig. 1c,d). We focused on leaf miners and gallers because they produce persistent, taxonomically diagnostic traces that remain identifiable in dried material, allowing for the assessment of species richness (Tooker & Giron 2020). In contrast, free-feeding herbivores leave non-diagnostic damage patterns, whilst sucking/piercing insects and pathogens would require sampling at specific activity periods or specialised preservation methods. Leaf miners and gallers were identified at the species level when possible, and otherwise to the genus level when species identification was not feasible due to the structural characteristics of the mines and galls. Identification of leaf miners was guided by the resources "Plant Parasites of Europe" (https://bladmineerders.nl/) and "British Leaf Miners" (http://www.leafmines.co.uk/), and gallers were identified using "British Plant Galls" (Redfern et al. 2002) and "Plant Parasites of Europe" (https://bladmineerders.nl/). The species richness of these leaf insects was estimated by summing the number of miner and galler taxa for each tree. Twenty-two of the 24 species are specialised to feed exclusively on oak (Mitchell et al. 2019).

Vascular plant species richness

We surveyed vascular plants between 1 and 10 August, 2022. To this end, four 0.5 m^2 circular plots were established around each of the seven randomly selected focal oak trees from the original ten trees in each site at a distance of five metres in the four cardinal directions, thus resulting in four plots per tree and a total of 252 plots. Hula hoops with a diameter of 80 cm were used as survey plots (Fig. S1). A photograph was taken of each plot from directly above using an iPhone 13 Pro Max at a height of 1.2 m, from which all vascular plants were identified to the lowest possible taxonomic level. Species were cross-checked with Mossberg and Stenberg (2003). Plants obscured by overlying vegetation were recorded when visible. Where species-level identification was not feasible (e.g., *Rubus* spp.), taxa were identified at the genus level. We aggregated vascular plant data to the tree level by summing the species in the four plots below the tree. In addition to the species recorded in these plots, shrub (e.g. hazel) and tree species richness surrounding each tree were assessed using the point relascope method with a prism factor of one (Bitterlich 1984). The richness of these surrounding shrub and tree species was then added to the sum of plant species associated with each specific oak tree.

Arthropod species richness, abundance, composition and biomass

To assess whether and how the overall arthropod biodiversity of the forest (species richness, abundance,

community composition and biomass) differed depending on oak species at the location, we surveyed arthropods using Malaise traps (Fig. 1e). For this, we deployed one Malaise trap in the centre of each of the nine locations, and two samples were collected from each site. Two collection periods were selected to bracket peak spring and late-summer activity from 6 May to 28 June 2022 and from 31 July to 19 October 2022. April sampling was not logistically feasible, and unfortunately, some traps malfunctioned in July, so we had to discard that period. The shaded forest locations prevented ethanol evaporation—collection bottles contained sufficient ethanol at retrieval. We found no statistical differences between seasonal samples, justifying their combination for analysis. The samples were preserved in 90% ethanol. The malaise traps were Watkins & Doncaster type (UK), 1.7 m long, 1.2 m wide, with a trap height of 1.7 m at the entrance, and a rear height of 0.95 m (Fig. 1e). All traps were of identical design, with collection heights standardised at 1.2 m. Ethanol lasted throughout each collection period as the traps were placed in shade in forests. Each sample was filtered through two sieves (a 5.6 mm mesh size sieve followed by a 0.075 mm) to remove the ethanol and divide the arthropod specimens into two size fractions. Size sorting was performed to enhance species detection (Elbrecht et al. 2017). Arthropod biomass was then estimated by weighing both size fractions. Total arthropod abundance was quantified by counting individuals in weighed subsamples (0.24–0.34 g) and then scaling these counts to the entire sample using the total weight of each size fraction. The samples were then sent to the Canadian Centre for DNA Barcoding (CCDB) for metabarcoding of the mitochondrial cytochrome c oxidase I (COI) gene, which was subsequently used to obtain biodiversity estimates (Forsman et al. 2024).

Metabarcoding of Malaise trap catches

For the DNA metabarcoding, DNA extraction and amplification were performed following the CCDB standard protocols (Ivanova et al. 2006). COI amplicon libraries were constructed using the BF3 (5'-CCHGAYATRGCHTTYCCHCG-3') + BR2 (5'-TCDGGRTGNCCRAARAAYCA-3') primer pair (Elbrecht et al. 2019; Elbrecht & Leese 2017), incorporating triplicate PCR replicates (Braukmann et al. 2019; Steinke et al. 2022). Triplicate negative (without template) and non-biological synthetic positive controls were included on each 96-sample plate. Sequencing was conducted on an Illumina NovaSeq SP flowcell with 2×250 bp paired-end reads at the Centre for Applied Genomics in Toronto. Raw reads were received as paired-end merged demultiplexed fastq files. Primer sequences were trimmed using Cutadapt v4.4 with default settings, and sequences were processed with APSCALE v1.6.3 using default settings (Buchner et al. 2022). Quality filtering retained 418 ± 10 bp length sequences with a maximum expected error of one. Dereplicated reads were clustered into OTUs (Operational Taxonomic Units) based on 97% similarity, with chimeras removed. OTUs were further curated using the LULU algorithm to eliminate potential erroneous sequences. Taxonomic assignments were performed against the MIDORI 2 database v GB257 using a local BLAST tool in APSCALE. Assignments were made using the following thresholds: species $\geq$ 98%, genus $\geq$ 95%, family $\geq$ 90%, order $\geq$ 85% (Hleap et al. 2021). Conflicting taxonomies were resolved to the most recent common ancestor and verified manually. We applied a conservative filtering threshold of 0.005% read abundance within each sample to address potential tag-switching and cross-contamination. OTUs falling below this threshold were removed, and the maximum number of reads for each species detected in negative controls was subtracted from the corresponding samples (Keck et al. 2023). The dataset was filtered to retain only OTUs assigned to the phylum Arthropoda. PCR replicates and size fractions were merged to generate a single sample per site, with the number of OTUs serving as an estimate of species richness of arthropods.

Statistical analysis

To evaluate the effects of oak species on herbivory and species richness, we employed generalised linear mixed models (GLMMs) using the glmmTMB package version 1.1.9 (Brooks et al. 2017) in R version 4.4.3 (R Core Team 2024). Statistical significance was assessed using Type II Wald chi-square tests implemented in the car package version 3.1–3 (Fox et al. 2019). Post-hoc pairwise comparisons between species were conducted using Tukey's Honest Significant Difference test implemented through the emmeans

package version 1.10.5 (Lenth 2023). To assess differences in community composition among oak species, we used Non-metric Multi-Dimensional Scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) using Bray–Curtis dissimilarity matrices (function 'adonis2' in the vegan package version 2.7–1 (Oksanen et al. 2025)). Due to the proportional nature of herbivory data (bounded between zero and one), we used beta regression designed explicitly for analysing proportions (Ferrari & Cribari-Neto 2004). The beta distribution accommodates the bounded nature of proportion data and can handle the heteroscedasticity and asymmetry typically present in such measurements (Cribari-Neto & Zeileis 2010). At the tree level, we fitted a beta regression mixed model with the proportion of herbivory as the response variable, oak species as a fixed effect, and site as a random effect to account for spatial dependencies. We used beta regression without random effects for site-level analysis, as herbivory was already averaged at the site level.

Species richness of leaf-feeding insects and vascular plants

The richness of leaf-feeding insects was analysed at both tree and site levels. At the tree level, we used a negative binomial GLMM with the number of leaf-feeding insect species (sum of leaf miners and gallers) as the response variable, oak species as a fixed effect, and site as a random effect. We combined leaf miners and gallers as they represent specialised herbivores that develop within plant tissues and show similar host specificity patterns (Tooker & Giron 2020). We used a negative binomial GLM at the site level without random effects, as data were already aggregated per site. Vascular plant species richness was similarly analysed using negative binomial models at both tree and site levels. For tree-level analysis, we fitted a GLMM with plant species richness as the response variable, oak species as a fixed effect, and site as a random effect. Site-level analysis used a negative binomial GLM without random effects. For all models, we verified the appropriateness of the negative binomial distribution for handling overdispersion in our count data. We used NMDS and PERMANOVA to assess community composition differences among oak species.

Arthropod species richness, abundance, community composition and biomass

We analysed oak species' effects on four aspects of arthropod communities at the site level. Arthropod species richness was assessed using OTU richness data. We analysed species richness using a negative binomial GLM to account for overdispersion in the count data. We used Gaussian GLMs with log-transformed data (using natural logarithm) to meet normality assumptions for arthropod abundance and biomass. The response variables were total biomass (g) and total number of individuals per Malaise trap. We also calculated Shannon diversity indices and visualised the OTU data using a Venn diagram. We used NMDS and PERMANOVA to assess community composition differences among oak species. For all models, oak species were included as a fixed effect.

Results

Leaf herbivory

Quercus rubra exhibited the highest herbivory ($8.70 \pm 1.18\%$; mean ± SE; $n = 21$ trees), followed by *Q. petraea* ($6.45 \pm 1.36\%$) and *Q. robur* ($5.63 \pm 1.02\%$), with each species sampled across three sites ($n = 21$ trees per species). At both the individual tree and site scale, no statistically significant effect of oak species on the level of leaf herbivory was found (tree: $\chi^2 = 4.48$, df = 2, $p = 0.107$; site: $\chi^2 = 2.73$, df = 2, $p = 0.255$) (Fig. 2a, b).

Endophytic insects

We identified 24 taxa of leaf miners and gallers across the nine sites and 63 trees (Table S1). *Trioza remota* was the most prevalent species, found at eight sites and on 44 trees, followed by *Neuroterus anthracinus*, present at six sites and on 26 trees. Six species were highly localised, each found on a single tree at one site (Supporting information 1). Oak species identity significantly influenced the richness of endophytic leaf-feeding insects at both the tree level ($\chi^2 = 46.765$, df = 2, $p < 0.001$) and site level scale ($\chi^2 = 14.179$, df = 2, $p < 0.001$) (Fig. 2c,d). At the tree level, *Q. robur* harboured the highest richness (mean ± SE: 5.19 ± 0.50 species per tree),

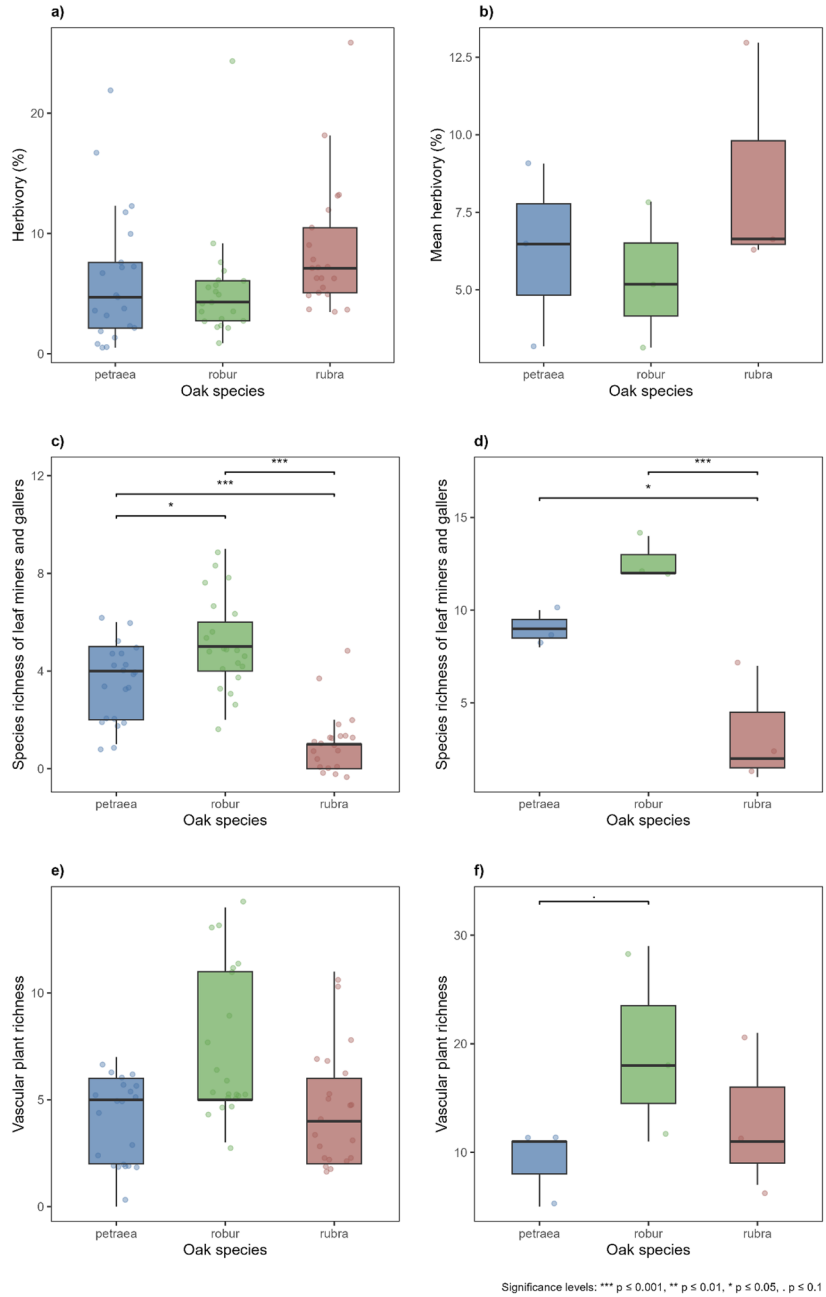

Fig. 2 Tree- and site-level herbivory, leaf-feeding insect richness, and vascular plant richness in different oak species sites. Tree-level measurements (a, c, e) represent individual trees (n = seven trees per site), while site-level measurements (b, d, f) represent site averages (n = three sites per oak species). **a**, **b** Leaf herbivory was measured as the mean percentage of leaf area removed by chewing insects assessed on 27 leaves per tree and averaged first at tree level and then at site level. **c**, **d** Leaf-feeding insect richness is measured as the number of unique gall and leaf-miner species. **e**, **f** Vascular plant richness is measured as the number of unique species in 0.5 m^2 plots, four beneath each tree, summing up to 21 plots per site. The boxplots show the median (horizontal line inside the box), first and third quartiles (box boundaries), and minimum and maximum values excluding outliers (whiskers). Individual points represent raw data from each tree or site. Box colours indicate oak species: *Quercus petraea* (blue), *Q. robur* (green), and *Q. rubra* (red). Asterisks indicate significance levels: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, $p \leq 0.1$. Statistical analyses were performed using beta regression for herbivory data (with logit link), negative binomial GLMMs for insect and plant richness (count data), and site as a random effect for tree-level analyses. Pairwise comparisons were conducted using Tukey's method with estimated marginal means

significantly higher than *Q. petraea* (3.48 ± 0.41 species per tree; $z = -2.65$, $p = 0.022$). The introduced *Q. rubra* supported the lowest richness (1.10 ± 0.23 species per tree), significantly lower than both *Q. petraea* (z = 4.83, $p < 0.001$) and *Q. robur* (z = 6.780, $p < 0.001$) (Fig. 2c). At the site level, similar patterns emerged. *Q. robur* sites supported the highest richness (mean ± SE: 12.67 ± 2.05 species per site), while *Q. rubra* sites had the lowest (3.33 ± 1.05 species per site). *Q. petraea* sites maintained intermediate richness (9.00 ± 1.73 species per site). Pairwise comparisons revealed significant differences between *Q. petraea* and *Q. rubra* ($z = 2.68$, $p = 0.020$) and between *Q. robur* and *Q. rubra* ($z = 3.76$, $p < 0.001$) (Fig. 2d). Regarding species composition, *Q. robur* had six unique species, *Q. rubra* had three unique species, and *Q. petraea* had one unique species. Due to the low number of leaf-feeding insect species on *Q. rubra*, statistical evaluation of community composition differences across oak species was not meaningful.

Vascular plants

In total, 63 unique plant species were recorded across all sampled trees, of which 23 were singletons. The most common plant taxa was *Rubus* spp (present at 30 trees across seven sites), followed by *Vaccinium myrtillus* (19 trees across four sites) and *Picea abies* (18 trees across six sites). At the tree level, the effect of oak species was not statistically significant ($\chi^2 = 3.37$, df = 2, $p = 0.185$), while at the site level, the analysis revealed a non-significant trend of oak species on vascular plant species richness ($\chi^2 = 5.38$, df = 2, $p = 0.068$), where *Q. robur* sites harboured the highest richness (Fig. 2e,f). Eight plant species were unique to *Q. petraea*, including *Calluna vulgaris*. Twenty-one species were unique to *Q. robur*, including *Anemone nemorosa*, and ten were unique to *Q. rubra*, including *Urtica dioica*. Eight species were shared across all three oak species. The composition of vascular plant communities did not differ significantly among oak species (PERMANOVA: $R^2 = 0.235$, $F_{2,6} = 0.920$, $p = 0.52$). The NMDS ordination supported this, which fit well with a low-stress value of 0.055 (Fig. S2).

Arthropod species richness, abundance, composition and biomass

Across the nine sites, an estimated 160,868 individuals with a combined weight of 749.55 g were collected, representing 5,089 OTUs (Operational Taxonomic Units, used as an estimate for species), where 2,391 (47.0%) were singletons (OTUs with only one read). Of the 5 089 OTUs detected (Table S2), 1 510 (30%) were resolved to species level, 485 (10%) to genus only, 1 316 (26%) to family, 1 153 (23%) to order, 619 (12%) to class, and 6 (< 0.1%) only to phylum (Table S2).

The number of OTUs did not differ significantly among oak species ($\chi^2 = 0.48$, df = 2, $p = 0.79$). Estimated OTU richness was similar across species: *Q. robur* (1,420 ± 106.0 OTUs per site), *Q. petraea* (1,373 ± 103.0 OTUs per site), and *Q. rubra* (1,322 ± 99.2 OTUs per site) (Fig. S4). There was no significant effect of oak species on arthropod abundance ($\chi^2 = 0.59$, df = 2, $p = 0.74$) or biomass ($\chi^2 = 0.05$, df = 2, $p = 0.98$). Estimated values for *Q. robur*, *Q. petraea*, and *Q. rubra* sites were comparable for both abundance (mean ± SE on log scale: 9.82 ± 0.195, 9.57 ± 0.195, and 9.79 ± 0.195, respectively) and biomass (mean ± SE on log scale: 4.50 ± 0.182, 4.39 ± 0.182, and 4.24 ± 0.182, respectively). The shared OTU pool included 1,159 OTUs (22.8%) across all three oak species. Among OTUs unique to a single oak species (2,595 OTUs, 51.0%), *Q. robur* harboured the highest number (1,015), followed by *Q. petraea* (857) and *Q. rubra* (723). The remaining 1,335 OTUs (26.2%) were shared between two oak species. Multivariate statistics revealed that OTU composition did not differ significantly among oak species (PERMANOVA: $R^2 = 0.21$, $F_{2,6} = 0.80$, $p = 0.88$, NMDS; stress = 0.059) (Fig. S3).

Discussion

Our study reveals that the identity of the oak species fundamentally shapes endophytic insect communities, with the native *Q. robur* and *Q. petraea* harbouring significantly higher species richness than the introduced *Q. rubra*. This pattern is consistent with the enemy release hypothesis (Keane & Crawley 2002), recently validated through meta-analysis (Xirocostas et al. 2023), which predicts that invasive plants can successfully establish

in new regions partly by escaping their co-evolved herbivores. The markedly lower species richness of endophytic insects on *Q. rubra* points to an important role of host specialisation in plant–insect interactions (Meijer et al. 2016), demonstrating how evolutionary history shapes contemporary community assembly. While release from specialised herbivores may promote the success of *Q. rubra* (Cook-Patton et al. 2014), this can significantly disrupt native food webs (Liu et al. 2024). Our results for leaf miners and gallers align with emerging research showing that non-native trees often support depauperate specialist herbivore communities (Hartley et al. 2010), highlighting the cascading effects that plant invasions may have on higher trophic levels (Bezemer et al. 2014).

An intriguing aspect of our findings is the contrasting patterns between endophytic leaf feeders and free-feeding herbivory. While *Q. rubra* had few endophytes (leaf miners and gallers), the level of leaf damage from free-feeding generalist insect herbivores was comparable to that of the two native oak species. While the enemy release hypothesis suggests that non-native species should experience reduced herbivory in their introduced range (Valdés-Correcher et al., 2022), our findings show similar free-feeding herbivory damage on non-native trees. This is in line with a recent cross-Atlantic tree-diversity experiment also including *Q. rubra* demonstrating persistent damage by generalist herbivores and higher leaf herbivory on the non-native oak tree (Berthelot et al. 2023). Our results indicate that *Q. rubra* can accommodate free-feeding insect herbivores despite simultaneously hosting fewer specialist endophytes. This pattern aligns with research showing that native generalist herbivores can utilise non-native species and provide resistance against plant invasions (Morrison & Hay 2011). DNA metabarcoding identified abundant generalist defoliators in the red oak forests, including the three moth species *Ptilodon capucinus* (Notodontidae), *Operophtera* spp. (Geometridae), and *Apoda limacodes* (Limacodidae) that successfully can exploit *Q. rubra* despite the absence of co-evolutionary history (Svensson 1993). This flexible host plant use by generalist herbivores (Ali & Agrawal 2012) may represent a crucial ecological filter that defines plant invasion success (Pearse et al. 2013; Pearse & Hipp 2009). As such, our present finding aligns with a growing body of evidence that the outcome of plant invasions depends on the balance between release from specialists and accumulation of generalist enemies (Schulz et al. 2019). The ability of congeneric species to share herbivores is well-documented (Burghardt et al. 2010). Our results support the hypothesis that phylogenetic relatedness facilitates herbivore host shifts.

In our study, the patterns of herbivory, endophytic insects, and vascular plant diversity varied between local (tree-level) and stand-level (site-level) assessments, underscoring the importance of scale when investigating invasion impacts (Chase & Knight 2013). We found that vascular plant species richness did not differ significantly among oak species at the individual-tree level. Yet, differences emerged when plant diversity was investigated at the site scale, in agreement with the notion that, in general, diversity patterns depend on the spatial scale at which it is inferred (Rahbek 2005). In our case, plant species richness likely accumulates in different ways in *Q. robur* than in *Q. petraea* forests due to differences in environmental filtering (Díaz-Maroto & Vila-Lameiro 2007; Gilliam 2007). That is *Q. petraea* forests likely have a similar composition of vascular plant species across its site. At the same time, *Q. robur* stands harbour a more varying composition of plant species. The finding of higher plant richness in *Q. robur* forests is also consistent with previous research, where sites dominated by *Q. robur* generally exhibited high understory plant richness and where *Q. petraea* forests support fewer plant species compared to other tree species (Brunet et al. 2011; Ellenberg 1988). The introduction of *Q. rubra*, which alters leaf litter chemistry and soil processes (Stanek et al. 2020), did not significantly change plant community composition or richness at our sites, which is in contrast to the negative effects of *Q. rubra* as described by (Woziwoda et al. 2014). Our results are consistent with the hypothesis that red oak may alter soil chemistry similarly to native oaks, rather than creating uniquely detrimental conditions. However, subtle or longer-term impacts cannot be excluded, particularly as non-native trees can trigger soil-mediated and indirect competitive effects on native vegetation (Castro-Díez et al., 2019). Future research that explicitly evaluates this scale dependence—combining tree-level, site-level, and landscape-level assessments—will help clarify how non-native tree introductions reshape forest understory diversity over time.

While the species richness of endophyte insect communities differed markedly according to oak species identity, all of the arthropod diversity metrics we

investigated (species richness, abundance, community composition and biomass) were similar across forest sites regardless of the dominant oak species. The maintenance of arthropod biodiversity in sites dominated by the introduced *Q. rubra*, together with the variable arthropod diversity seen among sites within oak species, suggests that arthropods overall respond more strongly to forest structural complexity than to tree species identity (Basset et al. 2015; Giannetti et al. 2022). The density of oak trees at each site, while not explicitly quantified in our study, likely contributes to this structural complexity and warrants future investigation. This result and conclusion aligns with habitat heterogeneity theory (Tews et al. 2004), which posits that landscape-level features often override species-specific effects for mobile organisms (Chmura 2020; Mahon et al. 2023). The different results that we obtained for specialist endophytes and the more general arthropods mirror the documented difference between sessile organisms (e.g., lichens, fungi) that show strong host specificity (Gustafsson et al. 2023; Southwood et al. 2004) and mobile taxa that respond primarily to structural habitat features (Sweaney et al. 2015). However, our small sample sizes (n = three sites per oak species) warrant caution when interpreting the results. The large proportion of non-target arthropods captured in our Malaise traps may have masked oak-specific patterns (Crowley et al. 2023). Future studies should consider targeted sampling methods for oak-associated arthropods to better assess species-specific impacts.

Conclusions and future directions

We examined patterns at tree and site levels and revealed that invasion impacts vary with spatial scales, feeding guild and organism mobility (Chase & Knight 2013; Poisot et al. 2011; Schulz et al. 2019), highlighting the importance of multi-taxon assessments in invasion ecology (Sapsford et al. 2020). Free-feeding herbivory on *Q. rubra* matched that on native oaks, suggesting that non-native oaks may provide resources for higher trophic levels to a similar degree as native oaks, but this effect is likely to be modified by differences in herbivore species composition and thus in the seasonal timing of resource abundances. Overall, arthropod communities did not differ between oak types, possibly owing to functional habitat redundancy (Gossner et al. 2013; Wardle & Peltzer 2017). However, the distinct, less diverse endophytic assemblages on *Q. rubra* relative to *Q. petraea* and *Q. robur* underscore the influence of evolutionary history on forest biodiversity (Keane & Crawley 2002) and show that specialist and generalist species are likely to be impacted differently by the introduction of non-native tree species. Importantly, our findings are specific to comparisons within the genus *Quercus* and should not be extrapolated to all plant invasions. The fact that an invasion by a plant closely related to local natives may not have severely impacted generalist herbivores does not mean that invasions by unrelated plants would not disrupt local food webs. We recommend conserving native oak stands, monitoring *Q. rubra* spread, exploring mixed-species strategies for climate adaptation and biodiversity conservation (Gustafsson et al. 2023), and prioritising long-term, multi-taxa studies for improved management (Pötzelsberger et al. 2020; Saul et al. 2013; Williams & Dumroese 2013). Given our limited landscape replication, broader geographical studies are needed to confirm these patterns.

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Author contributions MF, MH, AF and JS conceived and designed the study. MH coordinated field sampling. MF and MH conducted statistical analyses. MF, AF, and MH wrote the initial draft of the manuscript. RS, JS, LJ and AT contributed to subsequent revisions. All authors reviewed and approved the final manuscript.

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Declarations

Competing interest The authors declare that they have no financial or non-financial interests that might be perceived as influencing the submitted work. This includes any relevant financial interests, activities, relationships, or affiliations with any organisation or entity having a financial interest in or financial conflict with the subject matter discussed in the manuscript.

References

Ali JG, Agrawal AA (2012) Specialist versus generalist insect herbivores and plant defense. Trends Plant Sci 17:293–302

Avon C, Bergès L, Dumas Y, Dupouey J-L (2010) Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. For Ecol Manag 259:1546–1555

Basset Y, Cizek L, Cuénoud P, Didham RK, Novotny V, Ødegaard F, Roslin T, Tishechkin AK, Schmidl J, Winchester NN (2015) Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. PLoS ONE 10:e0144110

Berthelot S, Bauhus J, Dormann CF, Gravel D, Messier C, Nock CA, Paquette A, Reich PB, Fründ J (2023) Exotic tree species have consistently lower herbivore load in a cross-Atlantic tree biodiversity experiment. Ecology 104:e4070

Bezemer TM, Harvey JA, Cronin JT (2014) Response of native insect communities to invasive plants. Annu Rev Entomol 59:119–141

Bitterlich W (1984) The relascope idea relative measurements in forestry. Commonwealth Agricultural Bureaux, Wallingford

Braukmann TWA, Ivanova NV, Prosser SWJ, Elbrecht V, Steinke D, Ratnasingham S, de Waard JR, Sones JE, Zakharov EV, Hebert PDN (2019) Metabarcoding a diverse arthropod mock community. Mol Ecol Res 19:711–727

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Brunet J, Valtinat K, Mayr ML, Felton A, Lindbladh M, Bruun HH (2011) Understory succession in post-agricultural oak forests: habitat fragmentation affects forest specialists and generalists differently. For Ecol Manag 262:1863–1871

Buchner D, Macher T-H, Leese F (2022) APSCALE: advanced pipeline for simple yet comprehensive analyses of DNA metabarcoding data. Bioinformatics 38:4817–4819

Burghardt KT, Tallamy DW, Philips C, Shropshire KJ (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1:1–22

Castro-Díez P, Vaz AS, Silva JS, Van Loo M, Alonso Á, Aponte C, Bayón Á, Bellingham PJ, Chiuffo MC, DiManno N (2019) Global effects of non-native tree species on multiple ecosystem services. Biol Rev 94:1477–1501

Chase JM, Knight TM (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. Ecol Lett 16:17–26

Chmura D (2020) The spread and role of the invasive alien tree *Quercus rubra* (L.) in novel forest ecosystems in central Europe. Forests 11:586

Cook-Patton SC, LaForgia M, Parker JD (2014) Positive interactions between herbivores and plant diversity shape forest regeneration. Proc R Soc Lond B Biol Sci 281:20140261

Cribari-Neto F, Zeileis A (2010) Beta regression in R. J Stat Softw 34:1–24

Crowley LM, Ivison K, Enston A, Garrett D, Sadler JP, Pritchard J, MacKenzie AR, Hayward SA (2023) A comparison of sampling methods and temporal patterns of arthropod abundance and diversity in a mature, temperate, Oak woodland. Acta Oecol 118:103873

Díaz-Maroto IJ, Vila-Lameiro P (2007) Deciduous and semi-deciduous oak forests (*Quercus robur*, *Q. petraea* and *Q. pyrenaica*) floristic composition in the Northwest Iberian Peninsula. Biologia 62:163–172

Dyderski MK, Chmura D, Dylewski Ł, Horodecki P, Jagodziński AM, Pietras M, Robakowski P, Woziwoda B (2020) Biological flora of the British Isles: *Quercus rubra*. J Ecol 108:1199–1225

Eaton E, Caudullo G, Oliveira S, De Rigo D (2016) Quercus robur and Quercus petraea in Europe: distribution, habitat, usage and threats. Eur Atlas for Tree Species 14:160–163

Ekholm A, Tack AJ, Bolmgren K, Roslin T (2019) The forgotten season: the impact of autumn phenology on a specialist insect herbivore community on oak. Ecol Entomol 44:425–435

Elbrecht V, Leese F (2017) Validation and development of COI metabarcoding primers for freshwater macroinvertebrate bioassessment. Front Environ Sci 5:11

Elbrecht V, Peinert B, Leese F (2017) Sorting things out: assessing effects of unequal specimen biomass on DNA metabarcoding. Ecol Evol 7:6918–6926

Elbrecht V, Braukmann TW, Ivanova NV, Prosser SW, Hajibabaei M, Wright M, Zakharov EV, Hebert PD, Steinke D (2019) Validation of COI metabarcoding primers for terrestrial arthropods. PeerJ 7:e7745

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) Indicator values of plants in Central Europe. Scripta Geobot 18:9–166

Ellenberg H (1988) Vegetation ecology of central Europe. Cambridge University Press, Cambridge

Ennos R, Cottrell J, Hall J, O'Brien D (2019) Is the introduction of novel exotic forest tree species a rational response to rapid environmental change?–A British perspective. For Ecol Manag 432:718–728

Felton A, Petersson L, Nilsson O, Witzell J, Cleary M, Felton AM, Björkman C, Sang ÅO, Jonsell M, Holmström E (2020) The tree species matters: biodiversity and ecosystem service implications of replacing Scots pine production stands with Norway spruce. Ambio 49:1035–1049

Ferrari S, Cribari-Neto F (2004) Beta regression for modelling rates and proportions. J Appl Stat 31:799–815

Forsman A, Sunde J, Salis R, Franzén M (2024) Latitudinal gradients of biodiversity and ecosystem services in protected and non-protected oak forest areas can inform climate smart conservation. Geogr Sustain 5:647–659

Forzieri G, Dakos V, McDowell NG, Ramdane A, Cescatti A (2022) Emerging signals of declining forest resilience under climate change. Nature 608:534–539

Fox J, Weisberg S, Price B, Adler D, Bates D, Baud-Bovy G, & Bolker B (2019) Car: companion to applied regression. R package version 3.1–3. *Website:* http://cran.r-project.org/web/packages/car/index.html *[accessed 01 June 2019]*

Gebeyehu MN, Hirpo FH (2019) Review on effect of climate change on forest ecosystem. Int J Environ Sci Nat Res 17:126–129

Giannetti D, Schifani E, Castracani C, Spotti FA, Mori A, Grasso DA (2022) The introduced oak *Quercus rubra* and acorn-associated arthropods in Europe: an opportunity for both carpophagous insects and their ant predators. Ecol Entomol 47:515–526

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845–858

Gossner MM, Lachat T, Brunet J, Isacsson G, Bouget C, Brustel H, Brandl R, Weisser WW, Mueller J (2013) Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conserv Biol 27:605–614

Gustafsson L, Franzén M, Sunde J, Johansson V (2023) The non-native *Quercus rubra* does not substitute the native *Quercus robur* and *Q. petraea* as substrate for epiphytic lichens and bryophytes. For Ecol Manage 549:121482

Hämäläinen A, Runnel K, Mikusiński G, Himelbrant D, Fenton NJ, Lõhmus P (2023) Living trees and biodiversity. boreal forests in the face of climate change: sustainable management. Springer, Cham, pp 145–166

Hamann A, Wang T (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786

Hartley MK, Rogers WE, Siemann E (2010) Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. Arthropod Plant Interact 4:237–245

Hartmann H, Bastos A, Das AJ, Esquivel-Muelbert A, Hammond WM, Martínez-Vilalta J, McDowell NG, Powers JS, Pugh TA, Ruthrof KX (2022) Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annu Rev Plant Biol 73:673–702

Hleap JS, Littlefair JE, Steinke D, Hebert PDN, Cristescu ME (2021) Assessment of current taxonomic assignment strategies for metabarcoding eukaryotes. Mol Ecol Resour 21:2190–2203

Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Mol Ecol Notes 6:998–1002

Johnson MT, Bertrand JA, Turcotte MM (2016) Precision and accuracy in quantifying herbivory. Ecol Entomol 41:112–121

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Keck F, Couton M, Altermatt F (2023) Navigating the seven challenges of taxonomic reference databases in metabarcoding analyses. Mol Ecol Resour 23:742–755

Kozlov MV, Lanta V, Zverev V, Zvereva EL (2015) Background losses of woody plant foliage to insects show variable relationships with plant functional traits across the globe. J Ecol 103:1519–1528

Laux M, Lv H, Entling MH, Schirmel J, Narang A, Köhler M, Saha S (2022) Native pedunculate oaks support more biodiversity than non-native oaks, but non-native oaks are healthier than native oaks: A study on street and park trees of a city. Sci Total Environ 853:158603

Lenth R (2023) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8. 5

Liebhold AM (2012) Forest pest management in a changing world. Int J Pest Manag 58:289–295

Liu X, Huang W, Liu Y, Zhan A (2024) Perspectives of invasive alien species management in China. Ecol Appl 34:e2926

Mahon MB, Penn HJ, Campbell KU, Crist TO (2023) Differential patterns of taxonomic and functional diversity for two groups of canopy arthropods across spatial scales. Ecosphere 14:e4700

Májeková J, Medvecká J, Mikulová K, Slabejová D, Šibíková M, Zaliberová M, Škodová I (2024) Structure of forest stands of alien tree *Quercus rubra* in Central Europe. Biologia 79:1169–1176

Meijer K, Schilthuizen M, Beukeboom L, Smit C (2016) A review and meta-analysis of the enemy release hypothesis in plant–herbivorous insect systems. PeerJ 4:e2778

Merceron NR, Leroy T, Chancerel E, Romero-Severson J, Borkowski DS, Ducousso A, Monty A, Porté AJ, Kremer A (2017) Back to America: tracking the origin of European introduced populations of *Quercus rubra* L. Genome 60:778–790

Mitchell R, Bellamy P, Ellis CJ, Hewison R, Hodgetts N, Iason G, Littlewood N, Newey S, Stockan J, Taylor A (2019) Oakecol: a database of oak-associated biodiversity within the UK. Data Brief 25:104120

Morrison WE, Hay ME (2011) Herbivore preference for native vs. exotic plants: generalist herbivores from multiple continents prefer exotic plants that are evolutionarily naïve. PLoS ONE 6:e17227

Mossberg B, Stenberg L (2003) Den nya nordiska floran Andra tryckningen. Wahlström & Widstrand, Stockholm

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H. (2025) vegan: Community ecology package. R Package Version 2.7-1. Retrieved from https://cran.r-project.org/web/packages/vegan/index.html

Pearse IS, Hipp AL (2009) Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. Proc Natl Acad Sci U S A 106:18097–18102

Pearse IS, Harris DJ, Karban R, Sih A (2013) Predicting novel herbivore–plant interactions. Oikos 122:1554–1564

Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME (2011) A conceptual framework for the evolution of ecological specialisation. Ecol Lett 14:841–851

Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Høye TT, Ims RA, Jeppesen E, Klein DR, Madsen J, McGuire AD, Rysgaard S, Schindler DE, Stirling I, Tamstorf MP, Tyler Nicholas JC, van der Wal R, Welker J, Wookey PA, Schmidt NM, Aastrup P (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358

Pötzelsberger E, Spiecker H, Neophytou C, Mohren F, Gazda A, Hasenauer H (2020) Growing non-native trees in European forests brings benefits and opportunities but also has its risks and limits. Curr for Rep 6:339–353

Pureswaran DS, Roques A, Battisti A (2018) Forest insects and climate change. Curr for Rep 4:35–50

R Core Team (2024) R: a language and environment for statistical. R version 4.4.3, Vienna, Austria

Rahbek C (2005) The role of spatial scale and the perception of large-scale species-richness patterns. Ecol Lett 8:224–239

Redfern M, Shirley P, Bloxham M (2002) British Plant Galls: Identification of Galls on Plants and Fungi. Shrewsbury: FSC Publications.

Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD II, Green JL, Hulme PE, Nuñez MA, Orwin KH, Pauchard A, Wardle DA, Peltzer DA (2020) Towards a framework for understanding the context dependence of impacts of non-native tree species. Funct Ecol 34:944–955

Saul W-C, Jeschke J, Heger T (2013) The role of eco-evolutionary experience in invasion success. NeoBiota 17:57

Schulz AN, Lucardi RD, Marsico TD (2019) Successful invasions and failed biocontrol: the role of antagonistic species interactions. Bioscience 69:711–724

Southwood T (1961) The number of species of insect associated with various trees. J Anim Ecol. 30:1-8.J Anim Ecol. https://doi.org/10.2307/2109

Southwood TRE, Wint GW, Kennedy CE, Greenwood SR (2004) Seasonality abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. Eur J Entomol 101:43–50

Southwood TRE, Wint GW, Kennedy CE, Greenwood SR (2005) The composition of the arthropod fauna of the canopies of some species of oak (*Quercus*). Eur J Entomol 102:65–72

Stanek M, Piechnik Ł, Stefanowicz AM (2020) Invasive red oak (*Quercus rubra* L.) modifies soil physicochemical properties and forest understory vegetation. For Ecol Manage 472:118253

Steinke D, deWaard SL, Sones JE, Ivanova NV, Prosser SWJ, Perez K, Braukmann TWA, Milton M, Zakharov EV, deWaard JR, Ratnasingham S, Hebert PDN (2022) Message in a bottle-metabarcoding enables biodiversity comparisons across ecoregions. Gigascience. https://doi.org/10.1093/gigascience/giac040

Svensson I (1993) Lepidoptera-calender. Hans Hellberg, Stockholm

Sweaney N, Driscoll DA, Lindenmayer D, Porch N (2015) Plantations, not farmlands, cause biotic homogenisation of ground-active beetles in south-eastern Australia. Biol Conserv 186:1–11

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Thunes KH, Søli GE, Thuróczy C, Fjellberg A, Olberg S, Roth S, Coulianos C-C, Disney RHL, Starý J, Vierbergen G (2021) The arthropod fauna of oak (*Quercus* spp., Fagaceae) canopies in Norway. Diversity 13:332

Tooker JF, Giron D (2020) The evolution of endophagy in herbivorous insects. Front Plant Sci 11:581816

Tyler T, Karlsson T, Milberg P, Sahlin U, Sundberg S (2015) Invasive plant species in the Swedish flora: developing criteria and definitions, and assessing the invasiveness of individual taxa. Nord J Bot 33:300–317

Valdés-Correcher E, Popova A, Galmán A, Prinzing A, Selikhovkin AV, Howe AG, Mrazova A, Dulaurent AM, Hampe A, Tack AJM (2022) Herbivory on the pedunculate oak along an urbanization gradient in Europe: effects of impervious surface, local tree cover, and insect feeding guild. Ecol Evol 12:e8709

Voelkl B, Altman NS, Forsman A, Forstmeier W, Gurevitch J, Jaric I, Karp NA, Kas MJ, Schielzeth H, Van de Casteele T, Würbel H (2020) Reproducibility of animal research in light of biological variation. Nat Rev Neurosci 21:384–393

Wardle DA, Peltzer DA (2017) Impacts of invasive biota in forest ecosystems in an aboveground–belowground context. Biol Invasions 19:3301–3316

Williams MI, Dumroese RK (2013) Preparing for climate change: forestry and assisted migration. J for 111:287–297

Woziwoda B, Potocki M, Sagan J, Zasada M, Tomusiak R, Wilczyński S (2014) Commercial forestry as a vector of alien tree species-the case of *Quercus rubra* L. introduction in Poland. Balt for 20:131–141

Xirocostas ZA, Ollerton J, Tamme R, Peco B, Lesieur V, Slavich E, Junker RR, Pärtel M, Raghu S, Uesugi A (2023) The great escape: patterns of enemy release are not explained by time, space or climate. Proc R Soc Lond B Biol Sci 290:20231022

Xu W-B, Guo W-Y, Serra-Diaz JM, Schrodt F, Eiserhardt WL, Enquist BJ, Maitner BS, Merow C, Violle C, Anand M (2023) Global beta-diversity of angiosperm trees is shaped by Quaternary climate change. Sci Adv 9:eadd8553

Youngentob KN, Zdenek C, van Gorsel E (2016) A simple and effective method to collect leaves and seeds from tall trees. Methods Ecol Evol 7:1119–1123