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ORIGINAL RESEARCH

Low cross-taxon congruence and weak stand-age effects on biodiversity in Swedish oak forests

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Abstract

Assessing cross-taxon congruence is vital for effective forest conservation, because different taxonomic groups may respond inconsistently to key habitat variables such as stand age. We examined six taxonomic groups—insects, arachnids, springtails, epiphytic lichens, bryophytes, and vascular plants—across 25 Swedish oak stands ranging from 19 to 165 years old to determine whether species richness correlated among groups (cross-taxon congruence) and how it related to stand age. In total, we identified 22,276 unique taxa (with on average 4,128 per stand) using COI metabarcoding for arthropods and field surveys for lichens, bryophytes, vascular plants. Associations of species richness in each taxonomic group with richness in the others were weak, indicating low cross-taxon congruence. Only lichens showed a significant, positive relationship of species richness with stand age, while springtails exhibited a unimodal pattern, and the other four groups were unaffected by stand age. Although species composition in four groups changed with stand age, the explanatory power was generally low. Overall, the heterogeneous responses of different groups indicated by our findings caution against the use of single taxonomic groups or environmental variables as indicators and keys to successful protection of biodiversity. Instead, forest management strategies should adopt multi-taxon assessments and recognize the value of both younger and older stands to safeguard biodiversity in oak-dominated landscapes.

Keywords Arthropods · Biodiversity · Bryophytes · Conservation · Forest ecology · Lichens · Species richness · Vascular plants

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Introduction

The preservation of forests is crucial for global biodiversity, as forests provide diverse habitats supporting vast numbers of species. However, forest cover is declining rapidly in many parts of the world, with old-growth and mature forests being particularly vulnerable (Hansen 2000; Betts et al. 2017; Tinya et al. 2023). Older forests play key ecological roles in carbon storage, water regulation, and serve as reservoirs of specialized, disturbance-sensitive species (Lindenmayer et al. 2006; Gibson et al. 2011). Consequently, many have assumed that forest age is the primary determinant of biodiversity (Berg et al. 1994; Bengtsson et al. 2000; Lindenmayer et al. 2006; Hekkala et al. 2023), because older stands typically provide accumulated substrates and structural complexity that favour higher species richness (Harmon et al. 1986; Stokland et al. 2012; Storch et al. 2023; Parajuli and Markwith 2023; Zeller et al. 2023).

However, different taxonomic groups may respond differently to forest age, complicating broad generalizations (Hilmers et al. 2018). Dispersal limitations, habitat preferences, and species life-history traits all shape how any taxon might benefit—or not—from older forest conditions (Paillet et al. 2010; Johansson et al. 2012). Recognizing these differences is critical for designing inclusive and effective conservation strategies (Noss 1990; Bengtsson et al. 2000).

Evaluating cross-taxon congruence in species richness and composition is equally important (Westgate et al. 2014). Conservationists often rely on "indicator" or "surrogate" taxa, assuming that patterns of biodiversity in one group will reflect overall biodiversity (Rodrigues and Brooks 2007; Zeller et al. 2023). This approach can be appealing in forest ecosystems where extensive sampling is resource-intensive (Gao et al. 2015). Yet, many studies challenge the reliability of single-taxon indicators due to low congruence across taxa, even in the same habitat types (Wolters et al. 2006; Westgate et al. 2014). When different taxonomic groups respond differently to environmental gradients or management actions, a single group may poorly represent the consequences for the broader community (Hilmers et al. 2018; Tullus et al. 2022).

The aim of this study was to analyse the correlation in species richness among six major taxonomic groups (insects, arachnids, springtails, vascular plants, epiphytic lichens, and bryophytes) in oak forests of southern Sweden. We hypothesized that correlations between groups would be relatively weak due to their differing ecological demands, but species richness should generally increase with stand age, and species composition would shift accordingly.

Materials and methods

Study area

We conducted our study in southern Sweden, covering roughly 130,000 km² of mostly temperate and hemi-boreal vegetation zones (Fig. S1). The region is a patchwork of forests, farmland, and lakes, and encompasses the native range of oaks in Sweden. Oak (*Quercus robur*) represent a key species of high conservation interest, hosting an exceptionally rich biota (Ranius and Jansson 2000; Sverdrup-Thygeson et al. 2010; Johansson et al. 2012). In

southern Sweden, *Q. robur* often forms semi-natural stands, frequently managed for timber but historically maintained as wood-pastures. These stands can harbour a diverse assemblage of invertebrates, bryophytes, lichens, and vascular plants, some of which are specialised on old-growth structures such as large trunks, standing dead trees, and abundant coarse woody debris (Nilsson et al. 2002). Here we selected oak forests with forest production-oriented management regimes, which lack very old trees and may have more limited dead wood availability and structural heterogeneity.

In the study region, the production forests are dominated by spruce (*Picea abies*) and pine (*Pinus sylvestris*) plantations. Outside these, common deciduous trees are birch (*Betula* sp.), aspen (*Populus tremula*), alder (*Alnus glutinosa*), rowan (*Sorbus aucuparia*), beech (*Fagus sylvatica*), wych elm (*Ulmus glabra*), ash (*Fraxinus excelsior*), linden (*Tilia cordata*), maple (*Acer platanoides*), and goat willow (*Salix caprea*).

Estimation of tree and stand age

Twenty-five oak stands were selected in 2022 to represent a broad range of stand ages in production forests (Fig. S1, Table S1). All stands were subject to varying intensities of production forestry, characterised by periodic thinning, potential removal of dead wood, and limited regeneration gaps. We deliberately excluded pre-canopy closure stands as they represent transitional communities with high understory light availability that differ fundamentally from established forest ecosystems in structure and microclimate. In each stand, increment cores were collected from ten dominant (part of the upper canopy) *Quercus* individuals to determine stand age (mean age of the ten trees). Standard dendrochronological procedures were applied, including core preparation, tree-ring measurements, cross-dating, and error-checking with COFECHA (Holmes 1983; Fritts 1976; Bräker 2002). For samples missing the pith, estimates of missing rings were made, including adjustments for coring height (Drobyshev and Niklasson 2010).

Biodiversity quantification

We targeted six main taxonomic groups: vascular plants, bryophytes, lichens, insects, arachnids, and springtails. These groups were chosen to represent a wide range of functional groups including primary producers, pollinators, herbivores, predators, and detritivores, capturing a broad spectrum of habitat specialisations within oak forests (Cardoso et al. 2011; Gossner et al. 2013).

Vascular plants were recorded in August 2022 within a grid of four 0.5 m² vegetation plots around each of ten trees per stand (40 plots per stand). We identified all vascular plant species except grasses and sedges. Epiphytic lichens and bryophytes were surveyed in 2023 on the same ten oak trees per stand, from ground level to 2 m on the trunk (Gustafsson et al. 2023).

Arthropods (insects, arachnids, and springtails) were sampled from May 2022 to September 2023 using a single Malaise trap per stand. Despite potential sampling biases, particularly for ground-dwelling spiders and springtails (see discussion), our single-trap design was chosen to maintain consistency and minimise disturbance. Traps were emptied monthly, and samples were preserved in ethanol. After size-sorting large samples, the contents underwent metabarcoding at the Canadian Centre for DNA Barcoding (CCDB). DNA was extracted

following CCDB protocols (Ivanova et al. 2006), then the COI fragment was amplified using the BF3 + BR2 primer set (Elbrecht et al. 2019). Sequencing was performed on an Illumina Novaseq. Raw reads were merged, trimmed for primers using Cutadapt (Martin 2011), and processed with APSCALE (Buchner et al. 2022). OTUs were clustered at 97% similarity, with chimeras removed and the LULU algorithm applied to reduce erroneous sequences (Frøslev et al. 2017). Taxonomic assignment was made against the MIDORI 2 database (Leray et al. 2022). OTUs under a 0.005% read abundance threshold per sample were discarded to account for tag-switching or contamination. Triplicate PCRs and sample splits were merged, and only OTUs assigned to Arthropoda were retained.

Statistical analysis

All analyses were performed at the stand level. We assessed cross-taxon congruence by performing pairwise Pearson correlations of stand-level species richness (number of taxa) among the six taxonomic groups.

Species richness (number of taxa) per taxonomic group was modeled using generalized linear models (GLMs) with a negative binomial distribution (function *glm.nb* in the MASS package in R). Stand age, stand size, latitude, and longitude were included as predictors; for arthropods, total trap days were added to control for slight differences in sampling duration. For stand age we also included the squared term to capture potential unimodal relationships. Models were built based on AIC, where the final 'best model' was the one with the lowest AIC.

Species composition patterns were examined with nonmetric multidimensional scaling (NMDS), using *metaMDS* in R package vegan (Oksanen et al. 2019) with Bray–Curtis dissimilarities. Permutational multivariate ANOVA (PERMANOVA via *adonis2*) evaluated marginal effects of stand age, latitude, and longitude on species composition. All analyses were conducted in R v.4.2.2 (R Core Team 2023).

Results

Descriptive data

Stand ages (mean of ten oak trees) ranged from 19 to 165 years (mean = 83.0, SE = 8.5), Table S1 Individual trees spanned 13 to 190 years in age. Summing all species groups, we detected 22,276 unique taxa (20,630 insects, 962 arachnids, 316 springtails, 167 lichens, 46 bryophytes, 155 vascular plants). Across stands, the average total number of taxa was 4,128 (SE = 127.6). Insects were the most diverse (mean = 3,829 taxa per stand), followed by arachnids (159), springtails (72), lichens (34), bryophytes (10), and vascular plants (25).

Cross-taxon congruence

We found no significant correlations in species richness between any of the six taxonomic groups (Fig. 1). Pearson correlation coefficients ranged between −0.28 and 0.34, and none approached statistical significance ($p_{min} = 0.092$).

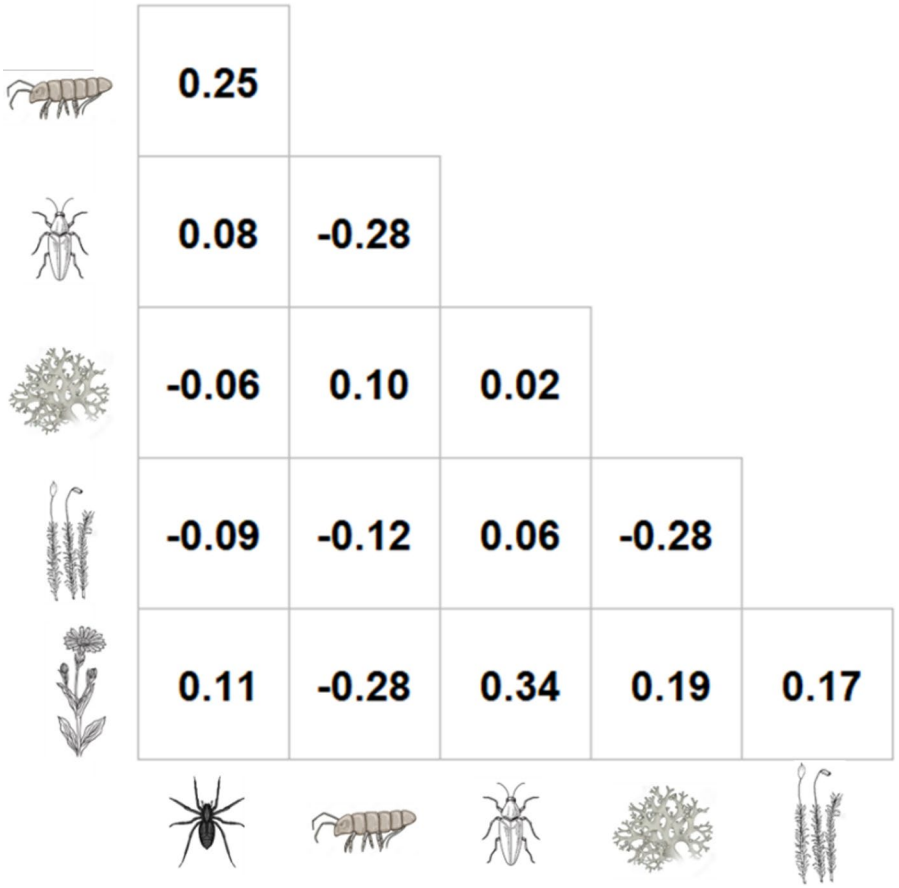

Fig. 1 The correlation coefficients (r) from Pearson correlations in species richness between the six taxonomic groups. None of the correlations were statistically significant ($p_{min} = 0.092$)

Species–age relationships

Only lichens showed a clear, positive association with stand age in terms of species richness (Fig. 2, Table S2). Springtails exhibited a unimodal relationship, peaking at intermediate stand ages. Arachnids, insects, bryophytes, and vascular plants showed no significant age–richness relationships. Stand age significantly affected species composition for arachnids, springtails, lichens, and vascular plants, but not for insects (Fig. 3, Table S3). However, the variation in composition explained by stand age was generally low ($R^2 < 0.1$), except for lichens ($R^2 = 0.17$). Geographic variables (longitude and latitude) also contributed to compositional variation across taxonomic groups (Table S3).

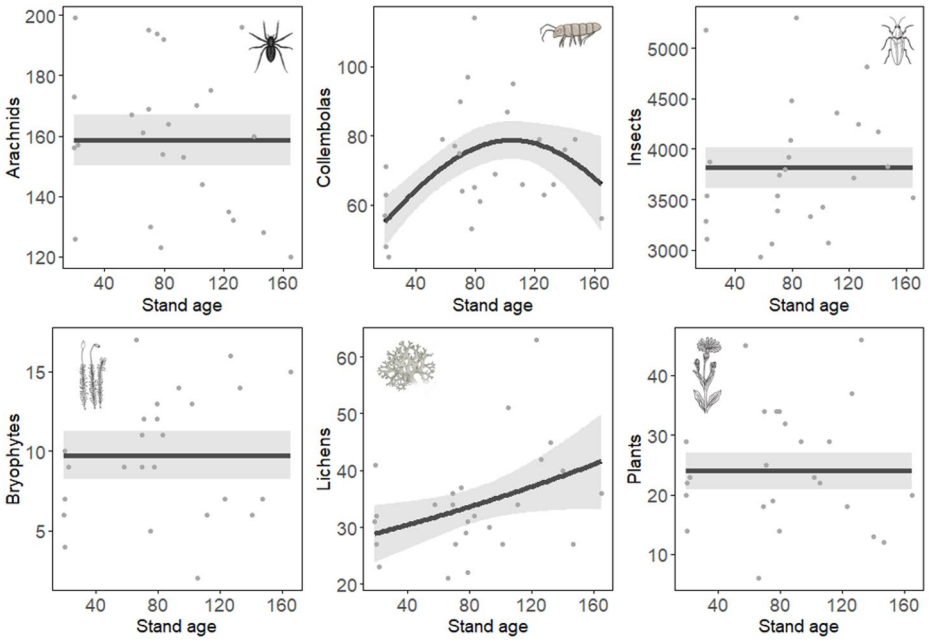

Fig. 2 The relationship between stand age (mean age from 10 dominant trees) and species richness (number of unique taxa) for six taxonomic groups. Black lines show model predictions with 95% confidence intervals (grey bands), and grey dots indicate raw data. Note that the scale of the y-axis differs between the panels

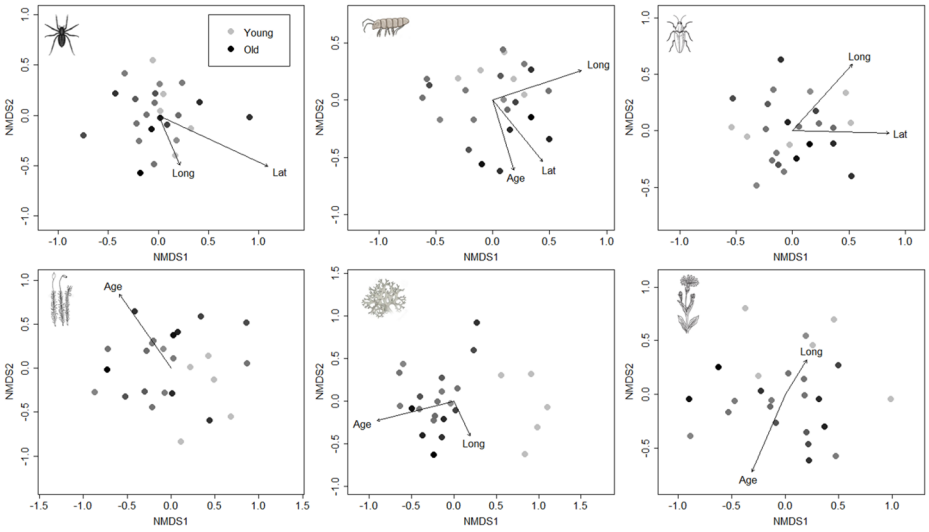

Fig. 3 The composition of unique taxa for the six taxonomic groups in relation to stand age, longitude, and latitude. The analyses of vascular plants and springtails required 3-dimensional NMDS to converge (stress < 0.2); however, only two dimensions are plotted for simplicity. Stand age is visualized as a gradient from light (young) to black (old) spanning the age range (19 to 165 years)

Discussion

Based on analyses of 22 276 unique taxa, our results reveal strikingly low cross-taxon congruence in Swedish oak forests, evident in the lack of correlation in species richness among the six taxonomic groups. This incongruence likely reflects that different taxa occupy divergent ecological niches, which may be shaped by variations in dispersal capabilities, habitat requirements, and life history strategies (Gossner et al. 2013; Westgate et al. 2014; Hilmers et al. 2018; Tullus et al. 2022). Our results agree with low congruence across taxa that has been reported from other ecosystems (Wolters et al. 2006; Kirkman et al. 2012; Westgate et al. 2014), indicating that single-taxon patterns often fail to capture the full spectrum of forest biodiversity (Rodrigues and Brooks 2007).

Our results also challenge the often-held belief that older forests inherently support higher biodiversity (Harmon et al. 1986; Bengtsson et al. 2000; Lindenmayer et al. 2006; Stokland et al. 2012). Four out of six species groups, comprising 98% of the species in this study, showed no clear relationship between stand age and species richness. Moreover, relatively little of the variation in species composition was explained by stand age for most groups. This is surprising as many species within these groups are dependent on substrates and structures that usually build up over time, such as large trees, coarse deadwood, and diverse canopy layers (Harmon et al. 1986; Johansson et al. 2009; Stokland et al. 2012; Storch et al. 2023; Parajuli and Markwith 2023). This suggests that large proportions of the species have broad niches and tolerances, high mobility, and ecological flexibility, allowing them to thrive across a range of different forest environments. Large-scale disturbances and younger forests may provide opportunities for many arthropods and vascular plants through increased resources, higher light availability, and reduced competition (Swanson et al. 2011; Lehnert et al. 2013). The only group with a clear increasing species richness and a change in composition with increasing stand age was lichens, which also agrees with earlier results showing that several specialized species have clear colonisation thresholds in oak age (Johansson et al. 2012).

Taken together, these findings suggest that relying on one or a few focal taxa or simple environmental proxies, such as stand age, risks oversimplifying complex ecological interactions (Kirkman et al. 2012; Prendergast et al. 2020), and from a practical standpoint, our results stress the need for multi-taxon or ecosystem-level assessments in forest management (Noss 1990; Rodrigues and Brooks 2007; Schall et al. 2020). We need to adopt broader monitoring schemes for a more accurate picture of overall biodiversity (Kati et al. 2004). Given the finite resources available for conservation, managers must balance cost and efficacy. However, prioritizing one taxon or a single stand variable may inadvertently exclude other facets of biodiversity, particularly in structurally diverse or successional-stage forests (Lindenmayer et al. 2006; Tullus et al. 2022). Addressing this gap may involve greater emphasis on functional traits, environmental gradients beyond stand age, or integrated sampling designs that track a suite of indicators representative of both mobile and sedentary taxa (Gossner et al. 2013; Hilmers et al. 2018).

Because regional species pools differ by two orders of magnitude across our focal taxa, the same absolute change in richness represents very different proportional changes. Although the correlation is scale-invariant, the larger relative sampling error for taxa with low richness (e.g. vascular plants and bryophytes) may reduce the statistical power and the maximum attainable correlation (Cardoso et al. 2011). Our study is further limited by the

exclusion of pre-canopy closure (< 15 years) and very old (> 200 years) stands, meaning we could not capture early successional communities associated with high light availability and the distinct communities documented in truly ancient stands (e.g. Ranius and Jansson 2000). However, our site selection accurately represents typical southern Swedish production forests, where our sampled mid-successional to mature stands reflect current forestry practices, though they may lack structures most critical for specialist species (Johansson et al. 2012; Ranius and Jansson 2000). Another potential limitation is our single-trap design for arthropods, especially for arachnids and springtails, for which the inclusion of pitfall traps would likely have increased the species numbers (Churchill and Arthur 1999). Moreover, the vascular plant survey only covered 20 m^2 in total and excluded grasses and sedges. Consequently, caution is warranted in interpreting absolute species richness for these groups (Southwood and Henderson 2000). However, while we may underestimate absolute diversity, the relative patterns we report still offer valuable information on cross-taxon relationships.

In conclusion, our findings reinforce that "one-size-fits-all" conservation strategies rarely capture the heterogeneity of different species groups, and robust forest policies therefore require multi-taxon assessments. Our results also advocate for a forest management strategy that values both young and old forests (Gustafsson and Perhans 2010; Schall et al. 2020). While many specialized species benefit from conservation efforts focused on preserving older stands with unique niches (Bengtsson et al. 2000; Lindenmayer et al. 2006; Hekkala et al. 2023; Zeller et al. 2023), we suggest a more nuanced approach for overall biodiversity that also embraces the importance of young forest stands. This may also allow for a more cost-effective preservation of biodiversity across taxa (Lundström et al. 2011). Recognizing that different taxonomic groups have different environmental requirements, and that both young and old forests contribute complementary ecological values may ensure the long-term sustainability of oak-dominated landscapes and align with adaptive forest management principles.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-025-03093-y.

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Author contributions VJ, AF, LG, and MF formulated the idea and developed the methodology. MH, JE, AF, and JS collected the data. RS did the molecular analysis and VJ the statistical analysis. VJ wrote the original draft. All authors reviewed and edited the manuscript.

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Data availability Data and code are available in the Figshare repository: https://doi.org/10.6084/m9.figshare.27100996.

Declarations

Competing interests The authors declare no competing interests.

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