



<http://www.diva-portal.org>

This is the published version of a paper published in *Biodiversity and Conservation*.

Citation for the original published paper (version of record):

Johansson, V., Forsman, A., Gustafsson, L., Hall, M., Edvardsson, J. et al. (2025)  
Low cross-taxon congruence and weak stand-age effects on biodiversity in Swedish oak  
forests

*Biodiversity and Conservation*, 34: 2739-2750

<https://doi.org/10.1007/s10531-025-03093-y>

Access to the published version may require subscription.

N.B. When citing this work, cite the original published paper.

Permanent link to this version:

<http://urn.kb.se/resolve?urn=urn:nbn:se:lnu:diva-139397>



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

Victor Johansson<sup>1</sup> · Anders Forsman<sup>2</sup> · Lena Gustafsson<sup>3</sup> · Marcus Hall<sup>2</sup> · Johannes Edvardsson<sup>4</sup> · Romana Salis<sup>2</sup> · Johanna Sunde<sup>2</sup> · Markus Franzén<sup>1,2</sup>

Received: 10 February 2025 / Revised: 8 May 2025 / Accepted: 9 May 2025 /

Published online: 2 June 2025

© The Author(s) 2025

## 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

---

Communicated by David Hawksworth.

---

Extended author information available on the last page of the article

## 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 km<sup>2</sup> 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 m<sup>2</sup> 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).

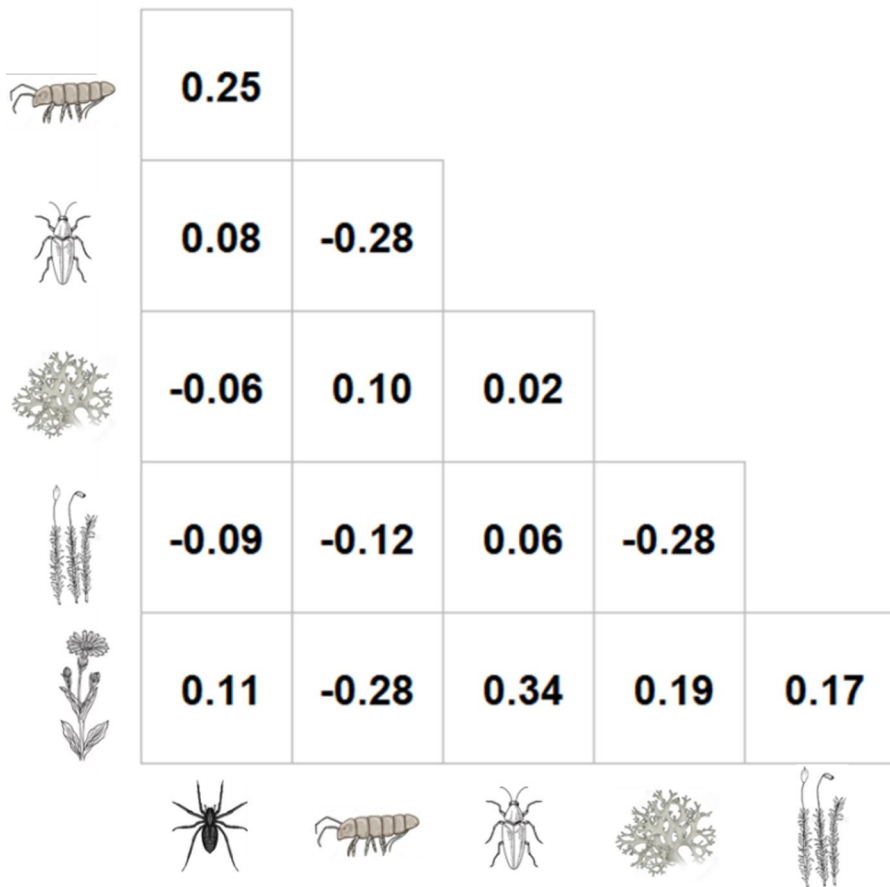
## Results

### 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

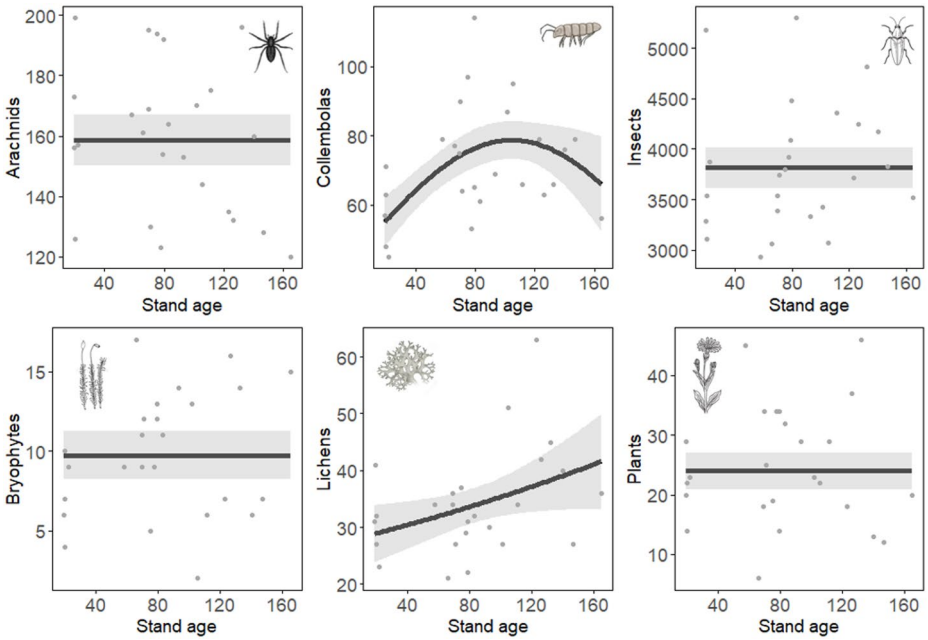
We found no significant correlations in species richness between any of the six taxonomic groups (Fig. 1). Pearson correlation coefficients ranged between  $-0.28$  and  $0.34$ , and none approached statistical significance ( $p_{\min} = 0.092$ ).



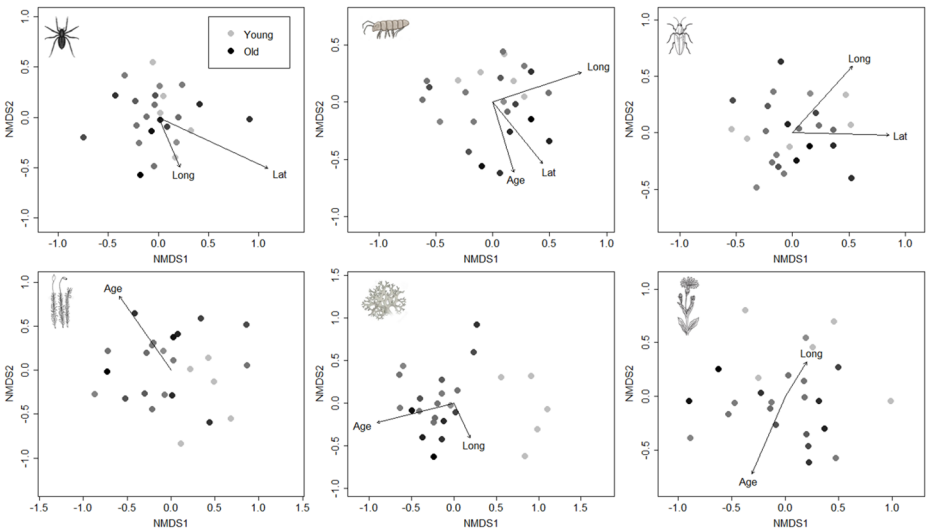
**Fig. 1** The correlation coefficients ( $r$ ) from Pearson correlations in species richness between the six taxonomic groups. None of the correlations were statistically significant ( $p_{\min} = 0.092$ )

### 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<sup>2</sup> 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>.

**Acknowledgements** We thank the landowners and extend our gratitude to Jonas Lundqvist, Sara Forsman, Ola Hammarström, and Raul Vicente for invaluable field assistance.

**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.

**Funding** Open access funding provided by Linköping University.

This work was financed by the Swedish Research Council for Sustainable Development, Formas (to MF, AF, VJ, JS, and LG; Dnr. 2021–02142), Stiftelsen Seydlitz MP Bolagen, Erik and Ebba Larssons Foundation, and Thure Rignells Foundation (to M.F.).

**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.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License,

which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References


- Bengtsson J, Nilsson SG, Franc A, Menozzi P (2000) Biodiversity, disturbances, ecosystem function, and management of European forests. *Ecol Manag* 132:39–50
- Berg Å, Ehnström B, Gustafsson L, Hallingbäck T, Jonsell M, Weslien J (1994) Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conserv Biol* 8:718–731
- Betts MG, Wolf C, Ripple WJ, Phalan B, Millers KA, Duarte A, Butchart SHM, Levi T (2017) Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* 547:441–444
- Bräker OU (2002) Measuring and data processing in tree-ring research – a methodological introduction. *Dendrochronologia* 20:203–216
- Buchner D, Macher T-H, Leese F (2022) APSCALE: advanced pipeline for simple yet comprehensive analyses of DNA metabarcoding data. *Bioinformatics* 38:4817–4819
- Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. *Biol Conserv* 144:2647–2655
- Churchill TB, Arthur JM (1999) Measuring spider richness: effects of different sampling methods and Spatial and Temporal scales. *J Insect Conserv* 3:287–295
- Drobyshev I, Niklasson M (2010) How old are the largest Southern Swedish Oaks?? A dendrochronological analysis. *Ecol Bull* 53:155–163
- Elbrecht V, Braukmann TWA, Ivanova NV, Prosser SWJ, Hajibabaei M, Wright M, Zakharov EV, Hebert PDN, Steinke D (2019) Validation of COI metabarcoding primers for terrestrial arthropods. *PeerJ* 7: e7745. <https://doi.org/10.7717/peerj.7745>
- Fritts HC (1976) *Tree rings and climate*. Academic, London
- Frøslev TG, Kjølner R, Bruun HH, Ejrnæs R, Brunbjerg AK, Pietroni C, Hansen AJ (2017) Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. *Nat Commun* 8:1188
- Gao T, Nielsen AB, Hedblom M (2015) Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecol Indic* 57:420–434
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–381
- Gossner MM, Lachat T, Brunet J, Isacson G, Bouget C, Brustel H, Brandl R, Weisser WW, Müller 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, Perhans K (2010) Biodiversity conservation in Swedish forests: ways forward for a 30-year-old multi-scaled approach. *Ambio* 39:546–554
- 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. *Ecol Manag* 549:121482
- Hansen RA (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81:1120–1132
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. In: MacFadyen A, Ford ED (eds) *Advances in Ecological Research*. Academic Press, pp 133–302
- Hekkala A-M, Jönsson M, Kärvelo S, Strengbom J, Sjögren J (2023) Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecol Indic* 148:1110069
- Hilmers T, Friess N, Bässler C, Heurich M, Brandl R, Pretzsch H, Seidl R, Müller J (2018) Biodiversity along temperate forest succession. *J Appl Ecol* 55:2756–2766

- Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull* 43:69–78
- Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Mol Ecol Notes* 6:998–1002
- Johansson V, Bergman KO, Lättman H, Milberg P (2009) Tree and site quality preferences of six epiphytic lichens growing on Oaks in South Eastern Sweden. *Ann Bot Fenn* 46:496–506
- Johansson V, Ranius T, Snäll T (2012) Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. *Ecology* 93:235–241
- Kati V, Devillers P, Dufrière M, Legakis A, Vokou D, Lebrun P (2004) Testing the value of six taxonomic groups as biodiversity indicators at a local scale. *Conserv Biol* 18:667–675
- Kirkman LK, Smith LL, Quintana-Ascencio PF, Kaeser MJ, Golladay SW, Farmer AL (2012) Is species richness congruent among taxa? Surrogacy, complementarity, and environmental correlates among three disparate taxa in geographically isolated wetlands. *Ecol Indic* 18:131–139
- Lehnert LW, Bässler C, Brandl R, Burton PJ, Müller J (2013) Conservation value of forests attacked by bark beetles: highest number of indicator species is found in early successional stages. *J Nat Conserv* 21:97–104
- Leray M, Knowlton N, Machida RJ (2022) MIDORI2: A collection of quality controlled, preformatted, and regularly updated reference databases for taxonomic assignment of eukaryotic mitochondrial sequences. *Environ DNA* 4:894–907
- Lindenmayer DB, Franklin JF, Fischer J (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol Conserv* 131:433–445
- Lundström J, Öhman K, Perhans K, Rönnqvist M, Gustafsson L (2011) Cost-effective age structure and geographical distribution of boreal forest reserves. *J Appl Ecol* 48:133–142
- Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet J* 17:10–12
- Nilsson SG, Niklasson M, Hedin J, Aronsson G, Gutowski JM, Linder P, Ljungberg H, Mikusiński G, Ranius T (2002) Densities of large living and dead trees in old-growth temperate and boreal forests. *Ecol Manag* 161:189–204
- Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conserv Biol* 4:355–364
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) *vegan*: Community Ecology Package. <http://cran.r-project.org/web/packages/vegan/index.html>. Accessed 8 May 2025
- Paillet Y, Berges L, Hjältén J, Odor P, Avon C, Bernhardt-Römermann M, Bijlsma R-J, de Bruyn L, Fuhr M, Grandin U, Kanka R, Lundin L, Luque S, Magura T, Matesanz S, Mészáros I, Sebastiá M-T, Schmidt W, Standovář T, Tóthmérész B, Uotila A, Valladares F, Vellak K, Virtanen R (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv Biol* 24:101–112
- Parajuli R, Markwith SH (2023) Quantity is foremost but quality matters: A global meta-analysis of correlations of dead wood volume and biodiversity in forest ecosystems. *Biol Conserv* 283:110100
- Prendergast KS, Menz MHM, Dixon KW, Bateman PW (2020) The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere* 11:e03076
- R Core Team (2023) *R: a Language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old Oaks. *Biol Conserv* 95:85–94
- Rodrigues AS, Brooks TM (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu Rev Ecol Evol Syst* 38:713–737
- Salamon J-A, Scheu S, Schaefer M (2008) The Collembola community of pure and mixed stands of Beech (*Fagus sylvatica*) and Spruce (*Picea abies*) of different age. *Pedobiologia* 51:385–396
- Schall P, Heinrichs S, Ammer C, Ayasse M, Boch S, Buscot F, Fischer M, Goldmann K, Overmann J, Schulze E-D, Sikorski J, Weisser WW, Wubet T, Gossner MM (2020) Can multi-taxa diversity in European Beech forest landscapes be increased by combining different management systems? *J Appl Ecol* 57:1363–1375
- Southwood TRE, Henderson PA (2000) *Ecological methods*. Blackwell Science, Oxford
- Stokland JN, Siitonen J, Jonsson BG (2012) *Biodiversity in dead wood*. Cambridge University Press, New York
- Storch F, Boch S, Gossner MM, Feldhaar H, Ammer C, Schall P, Polle A, Kroiher F, Müller J, Bauhus J (2023) Linking structure and species richness to support forest biodiversity monitoring at large scales. *Ann Sci* 80:3
- Sverdrup-Thygesen A, Skarpaas O, Ødegaard F (2010) Hollow Oaks and beetle conservation: the significance of the surroundings. *Biodivers Conserv* 19:837–852

- Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front Ecol Environ* 9:117–125
- Tinya F, Doerfler I, de Groot M, Heilman-Clausen J, Kovács B, Márell A, Nordén B, Aszalós R, Bässler C, Brazaitis G, Burrascano S, Camprodon J, Chudomelová M, Čížek L, D'Andrea E, Gossner M, Halme P, Hédl R, Korboulesky N, Kouki J, Kozel P, Löhmus A, López R, Máliš F, Martín JA, Matteucci G, Mattioli W, Mundet R, Müller J, Nicolas M, Oldén A, Piqué M, Preikša Ž, Rovira Ciuró J, Remm L, Schall P, Šebek P, Seibold S, Simončič P, Ujházy K, Ujházyová M, Vild O, Vincenot L, Weisser WW, Ódor P (2023) A synthesis of multi-taxa management experiments to guide forest biodiversity conservation in Europe. *Glob Ecol Conserv* 46:e02553. <https://doi.org/10.1016/j.gecco.2023.e02553>
- Tullus T, Lutter R, Randlane T, Saag A, Tullus A, Oja E, Degtjarenko P, Pärtel M, Tullus H (2022) The effect of stand age on biodiversity in a 130-year chronosequence of *Populus tremula* stands. *Ecol Manag* 504:119833
- Westgate MJ, Barton PS, Lane PW, Lindenmayer DB (2014) Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nat Commun* 5:3899
- Wolters V, Bengtsson J, Zaitsev AS (2006) Relationship among the species richness of different taxa. *Ecology* 87:1886–1895
- Zeller L, Förster A, Keye C, Meyer P, Roschak C, Ammer C (2023) What does literature tell Us about the relationship between forest structural attributes and species richness in temperate forests? – A review. *Ecol Indic* 153:110383

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

## Authors and Affiliations

Victor Johansson<sup>1</sup>  · Anders Forsman<sup>2</sup> · Lena Gustafsson<sup>3</sup> · Marcus Hall<sup>2</sup> · Johannes Edvardsson<sup>4</sup> · Romana Salis<sup>2</sup> · Johanna Sunde<sup>2</sup> · Markus Franzén<sup>1,2</sup>

✉ Victor Johansson  
victor.a.johansson@liu.se

Anders Forsman  
anders.forsman@lnu.se

Lena Gustafsson  
lena.gustafsson@slu.se

Marcus Hall  
marcus.hall@lnu.se

Johannes Edvardsson  
johannes.edvardsson@geol.lu.se

Romana Salis  
romana.salis@lnu.se

Johanna Sunde  
johanna.sunde@lnu.se

Markus Franzén  
markus.franzen@liu.se

<sup>1</sup> Department of Physics, Chemistry and Biology (IFM), Linköping University, Linköping SE-581 83, Sweden

<sup>2</sup> Department of Biology and Environmental Science, Linnaeus University, Kalmar SE-391 82, Sweden

<sup>3</sup> Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala SE-750 07, Sweden

---

<sup>4</sup> Laboratory for Wood Anatomy and Dendrochronology, Department of Geology, Lund University, Sölvegatan 12, Lund 223 62, Sweden