



Original research article

Tree species influence the assemblages of trunk-dwelling arthropods and saproxylic beetles on fire-damaged trunks in a boreo-nemoral forest

Markus Franzén^{a,b,*}, Anders Forsman^b, Olof Persson^b

^a Department of Physics, Chemistry and Biology (IFM), Linköping University, Linköping SE-581 83, Sweden

^b Centre for Ecology and Evolution in Microbial Model Systems (EEMiS), Department of Biology and Environmental Science, Linnaeus University, Kalmar SE-391 82, Sweden

ARTICLE INFO

Keywords:

Arthropod communities

Beetle host specificity

Fire ecology

Saproxylic insects

Species turnover

Trunk traps

ABSTRACT

Wildfire is the dominant natural disturbance in boreal ecosystems, yet the extent to which recently burned trees of different species filter arthropod assemblages remains unclear. We quantified trunk-ascending arthropods and saproxylic beetles on fire-damaged trunks of four common boreal trees – *Betula pubescens*, *Populus tremula*, *Pinus sylvestris* and *Quercus robur* – in a 2021 burn in south-eastern Sweden. Twelve collar traps (three per species) operating for 189 days captured 9178 arthropods from 16 higher taxa, including 1427 beetles (96 species, 13 of which are red-listed). The overall arthropod assemblage varied only weakly with host tree and was primarily driven by Collembola, whereas beetle composition differed markedly, with host species identity explaining 52 % of the multivariate variation. *B. pubescens* supported the highest beetle richness (52 species) and *P. tremula* the greatest abundance (848 individuals, 60 %). Species turnover among hosts was high (Jaccard similarity = 0.17–0.36). Thirty beetle species, among them the Vulnerable *Dircaea australis* and Near-Threatened *Triplax rufipes*, showed significant preferences for a single tree species. Thus, post-fire trunks retain strong host specificity for beetles but not for the broader arthropod fauna; conserving a mosaic of burned stems across multiple tree species will maximise beetle richness and retain threatened taxa.

1. Introduction

Boreal forests are structured by recurrent wildfires, which reset succession, recycle nutrients and create habitat mosaics (de Groot et al., 2013, Flannigan et al., 1998, Seidl et al., 2020). Modern fire suppression and a warming climate are altering both the frequency and severity of these events, with uncertain long-term consequences for biodiversity (Schimmel and Granström, 1996). Although burned stands are often regarded as degraded, they can act as refugia for specialised and red-listed species that depend on open, sun-exposed wood, and charred substrates (Bond and Keeley, 2005, Certini, 2005). Arthropods – accounting for most forest animal diversity – respond rapidly to such structural changes, yet their host-tree associations after fires are poorly resolved. Beetles (Coleoptera) contribute disproportionately to decomposition, nutrient cycling, and pollination (Ulyshen and Šobotník, 2018, Weisser and Siemann, 2004). Within this order, saproxylic species that depend on dead or dying wood are especially diverse and sensitive to forest

* Corresponding author at: Department of Physics, Chemistry and Biology (IFM), Linköping University, Linköping SE-581 83, Sweden.
E-mail address: markus.franzen@liu.se (M. Franzén).

continuity (Seibold et al., 2015, Stokland and Meyke, 2008). Charred stands provide a transient pulse of dead wood, attracting both typical bark- and wood-inhabiting beetles and a wider arthropod guild that uses trunks for microclimate, forage, or vertical dispersal (Fredriksson et al., 2020, Wikars, 2002). Consequently, analyses of both the full arthropod assemblage and the beetle subset may help distinguish general from saproxylic responses.

Tree species differ in bark thickness, chemistry and decay trajectories, creating discrete microhabitats for associated biodiversity such as insects (Brunet et al., 2010, Šebek et al., 2016). Many beetles show narrow host requirements, whereas others exploit several hosts with weak preferences (Brin and Bouget, 2018, Milberg et al., 2014). Post-fire conditions could relax these constraints if burning homogenises substrate quality, or accentuate them if mortality and bark injury vary among tree hosts (Saint-Germain et al., 2004). Recent manipulations of dead wood confirm that substrate type, tree identity, and mortality agent jointly influence saproxylic beetle composition (Hägglund and Hjältén, 2018, Larsson Ekström et al., 2024). Yet empirical tests under natural fire remain scarce.

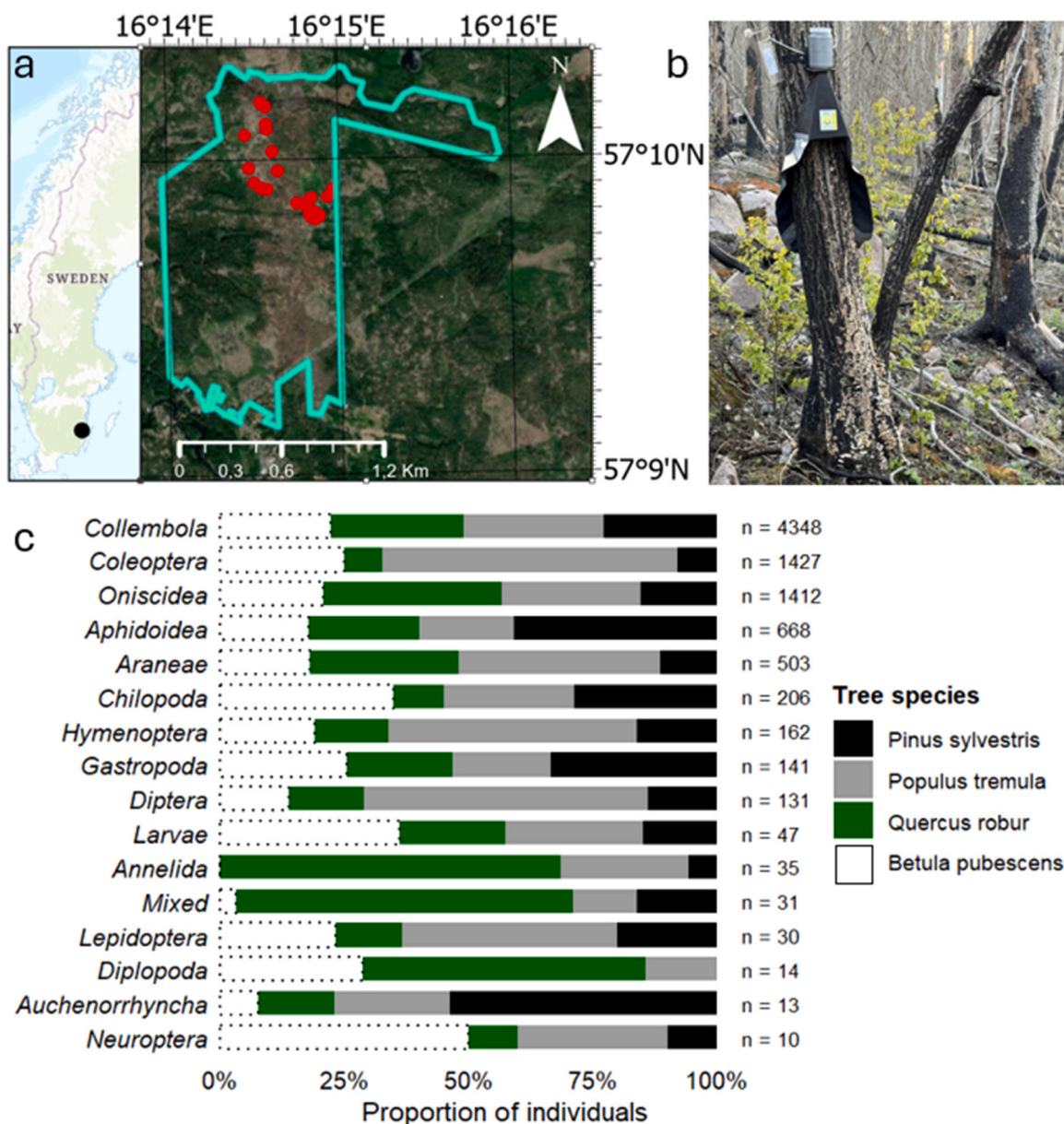


Fig. 1. Map and study site. (a) Map of Sweden (left) highlighting the location of the study area (black dot). Inset (right) shows a detailed aerial view of the Finsjöbrännan Nature Reserve (delineated in blue) and the trunk trap sites in red dots. (b) Trunk trap installed on an oak tree attacked by fungi. (c) Relative community composition of arthropods across the four tree species. Each bar represents the proportion of individuals belonging to different taxonomic groups sampled from burned trunks of *B. pubescens* (white with dotted outline), *P. sylvestris* (black), *P. tremula* (grey), and *Q. robur* (dark green). The total number of individuals (*n*) for each tree species is shown to the right of the bars.

Swedish boreal landscapes now experience fewer and smaller fires than before twentieth-century suppression, making every large burn ecologically valuable. The 200-ha Finsjöbrännan fire of June 2021, therefore, offers a timely opportunity to quantify early post-fire host specificity. We focus on four abundant tree species – the conifer *Pinus sylvestris* and the broadleaves *Populus tremula*, *Betula pubescens* and *Quercus robur* – that differ in bark combustibility, post-fire survival and decay dynamics.

Our study addresses three questions:

1. Do trunk-dwelling arthropod and saproxylic beetle assemblages differ among tree species after fire?
2. Which species of conservation concern colonise these early post-fire substrates?
3. Within the beetle community, do individual species exhibit significant host-tree preferences?

2. Methods

2.1. Study site

The Finsjöbrännan Nature Reserve (57° 10' 1.4" N, 16° 14' 18.1" E), is situated in the boreo-nemoral transition zone in south-eastern Sweden (Fig. 1a). It is a 200 ha large area that burned in June 2021 during a high-intensity crown-plus-surface fire. The climate is oceanic (Cfb) with 616 mm mean annual precipitation and mean daily temperatures of 0–2 °C (Dec–Feb) and 17–18 °C (Jun–Aug) (Swedish Meteorological and Hydrological Institute, SMHI). Before the fire, the stand was approximately fifty years old and the area was 85 % forested, with pine forest dominating (51 %), followed by spruce forest (20 %), and mixed forests (13 %). Non-forest areas covered 15 % including open land (13 %) and roads (2 %) (Agency, 2020, Nilsson et al., 2020). Granite outcrops and small wetlands fragmented the stand. All twelve study trunks were severely fire-scarred survivors selected in May 2024. All 12 trees had died by late August 2024. The arthropod assemblages sampled here therefore represent early post-fire colonists, along with a minor remnant fauna that survived in soil or rock refugia. From 2021–2024, 39 red-listed invertebrates have been reported and 57 red-listed taxa overall (Artportalen, www.artportalen.se download 22 July 2025). Further, a number of interesting and rare species have been reported from the area post fire (Johansson, 2024).

2.2. Sampling design

To characterise trunk-ascending assemblages, we installed twelve circular trunk collars at 1.3 m height (Fig. 1b). Collars were of polyethylene fixed with 15 mm stainless staples and sealed with neutral-cure silicone. The four host tree species – *P. sylvestris*, *P. tremula*, *B. pubescens*, and *Q. robur* – have contrasting bark traits, resin chemistry, and fire resilience, despite three being broadleaved and one coniferous. Each sampled tree met the criteria diameter at breast height ≥ 15 cm, height ≥ 7 m, and ≥ 70 % bark char. One trap was installed per tree ($n = 3$ per species). Traps were ≥ 15 m apart and distributed across the burn to span the severity gradient. Traps operated from 6 May to 1 December 2024 and were emptied on five dates (26 May, 7 July, 16 August, 20 September, 1 December). Catch pots contained 70 % propylene glycol plus a surfactant. Samples were stored at 4 °C pending processing. The modest replication reflects the limited number of comparably damaged stems and logistical constraints.

2.3. Sample processing and identification

Specimens were assigned to 16 higher taxa and life stages by a trained entomologist (Jonas Lundqvist, Vetlanda). All counts are reported; Collembola were retained at the order level because most individuals were immature and unidentifiable. Beetles were keyed to species following DyNTaxa (accessed 15 Jan 2025) and the Swedish Red List (Eide et al., 2020). Voucher specimens of rare or problematic taxa are deposited in the senior author's collection.

2.4. Data analysis

Analyses used to answer Q1: *Do trunk-dwelling arthropod and saproxylic beetle assemblages differ among tree species after fire?* We summed the number of individuals into 16 arthropod groups per tree, trap, and occasion, then modelled community composition using `manyglm()` from the `mvabund` package (Wang et al., 2012). Tree species was used as the predictor, with a negative binomial distribution to account for overdispersion. Model significance was evaluated via `anova.manyglm` to directly test whether tree species structures arthropod and beetle communities.

Multivariate ordination and PERMANOVA We explored differences in community composition among tree species using non-metric multidimensional scaling (NMDS) via `metaMDS()` from the `vegan` package (v2.5–7) (Oksanen et al., 2019), applying Bray–Curtis dissimilarities in two dimensions ($k = 2$) with a maximum of 100 iterations (`trymax = 100`). NMDS site scores were merged with the corresponding metadata, and species scores were used to identify influential taxa based on Euclidean distance from the origin. We then conducted a permutational multivariate analysis of variance (PERMANOVA) using `adonis2()` (9 999 permutations) to quantify the variance in community composition explained by tree species. Following the overall PERMANOVA, we performed pairwise comparisons between tree species using the `pairwiseAdonis` package with Bonferroni correction to identify which specific tree species pairs harboured significantly different beetle assemblages.

Analyses used to answer Q2: *Which species of conservation concern colonise these early post-fire substrates?* Species richness and sample coverage were estimated using the `iNEXT` package (v3.0.2) (Hsieh et al., 2016). Abundance data were aggregated by tree species and

converted into a matrix, then transformed into a list format, where each element contained non-zero abundances for a given tree species. We used `iNEXT()` with $q = 0$ (for species richness), `datatype = "abundance"`, an endpoint set to twice the maximum sample size for extrapolation, `knots = 40`, and `nboot = 1000` for bootstrap replicates. We then computed additional diversity metrics, including observed coverage, asymptotic richness, and richness at 95 % sample coverage using `estimateD()`. For red-listed species specifically, we calculated incidence rates with exact binomial confidence intervals to quantify colonisation success.

Analyses used to answer Q3: *Within the beetle community, do individual species exhibit significant host-tree preferences?* We constructed a bipartite matrix of beetle counts per tree species using `pivot_wider()`. The bipartite package (v2.15) (Dormann et al., 2008) was used to calculate network-level indices with `networklevel()` and species-level indices with `specieslevel()`, quantifying community-wide specialisation patterns. For beta diversity, we generated a site-by-species matrix and converted it to presence-absence format using `decostand(method = "pa")` from `vegan`. We then partitioned beta diversity into turnover and nestedness components using `beta.multi()` and `beta.pair()` from the `betapart` package (v1.6.0) (Baselga and Orme, 2012), employing the Jaccard similarity index as the similarity measure.

We visualised species overlap among different tree species using Venn diagrams created by `venn.diagram()` from the `VennDiagram` package (v1.6.20) (Chen and Boutros, 2011). To examine individual beetle host preferences, we calculated total abundance per beetle species and identified each species' preferred host as the tree with the highest abundance. Preference strength was defined as the ratio of maximum abundance on one tree to the total abundance across all trees. We applied chi-square goodness-of-fit tests to determine whether observed beetle distributions across tree species deviated significantly from uniform expectations, identifying species with significant host preferences.

3. Results

3.1. Overall arthropod and beetle diversity

Trunk collars yielded 9178 arthropods representing sixteen higher taxa; beetles comprised 1427 individuals (15.6 %) drawn from 96 species, thirteen of which were red-listed (seven Vulnerable, six Near Threatened, Fig. 2). The three numerically dominant groups were Collembola (4348), beetles (1427) and Oniscidea (1412), together constituting 78 % of the catch. Unexpected taxa included earthworms (Annelida, 35) and snails (Gastropoda, 134) ascending trunks (Fig. 1c).

3.2. Associations between tree species and total arthropod abundance

Populus tremula supported the highest arthropod abundance (3 088 individuals; mean \pm SD per tree = $1\,029 \pm 214$), followed by *Q. robur* ($2\,241$; 747 ± 102), *B. pubescens* ($2\,020$; 673 ± 188) and *P. sylvestris* ($1\,829$; 610 ± 55). Although total abundance varied among species, the multivariate generalised linear model detected only a marginally non-significant effect of host identity (Deviance = 220, $p = 0.092$). However, arthropod community composition differed significantly among tree species (Table 1). At the taxon level,

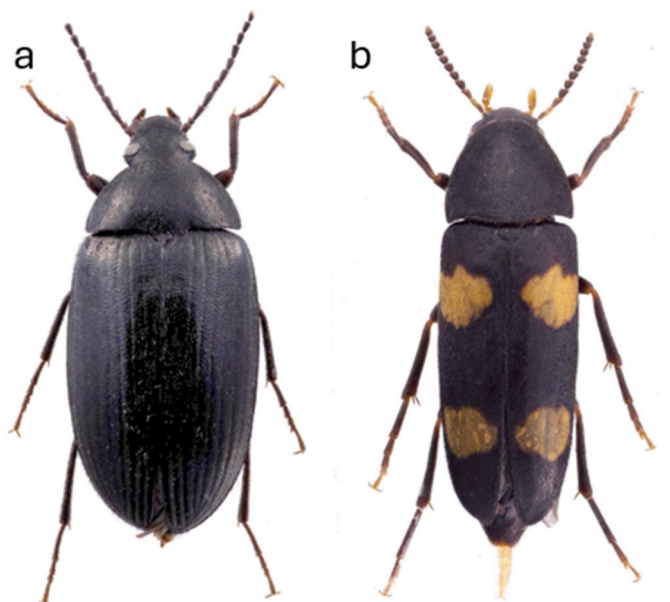


Fig. 2. Selected red-listed beetle species from the burned forest habitat of Finsjöbrännan Nature Reserve, southeastern Sweden. (a) *Prionychus melanarius* (Vulnerable), a specialist saproxylic species associated with *P. tremula*. (b) *Dircaea australis* (Vulnerable), a rare saproxylic species strongly associated with *B. pubescens*. Photographs by Olof Persson.

only Collembola exhibited a significant difference in abundance between hosts (Deviance = 44.4, $p = 0.049$; Table 2).

3.3. Associations between tree species and beetle assemblages

Rarefaction to 95 % coverage corroborated raw richness patterns: *Betula pubescens* 61.1 species (95 % CI 36.7–85.5), *Q. robur* 50.9 (26.5–75.3), *P. sylvestris* 46.6 (0–99.6) and *P. tremula* 30.1 (23.0–37.3) (Fig. 3). *Populus tremula* yielded the greatest beetle abundance (848 individuals; 283 ± 141 per tree) but only the second-highest richness (50 species). *Betula pubescens* supported the highest richness (52 species) at lower abundance (358 individuals; 119 ± 48). *Quercus robur* (109 individuals; 36 ± 15) and *P. sylvestris* (112; 37 ± 22) exhibited similar abundances but differed in richness (35 vs 26 species). Red-listed beetles were unevenly distributed: *Betula pubescens* hosted six species (24 individuals), *P. tremula* four (63), *P. sylvestris* four (4) and *Q. robur* three (6).

3.4. Community composition and multivariate patterns

NMDS on Bray–Curtis distances (stress = 0.13) separated beetle assemblages by host (Fig. 4). Pairwise PERMANOVA clarified the contribution of each host: *Quercus robur* differed significantly from the other three species ($p < 0.01$); *B. pubescens* differed from *P. tremula* ($p = 0.04$) and *P. sylvestris* ($p = 0.05$), whereas *P. tremula* and *P. sylvestris* did not differ ($p = 0.21$). The global model accounted for 52 % of the variance in community composition ($R^2 = 0.52$, $p = 0.002$).

3.5. Network structure and species overlap

A quantitative bipartite network (Fig. 5) contained 42 % of all potential links (connectance = 0.42). High web asymmetry (0.92) and the chi-square test ($\chi^2 = 9.36$, $df = 3$, $p = 0.025$) confirmed that these distributions differed significantly from uniform expectations—thirty of ninety-six species exhibited significant host tree preferences (Table 3). The network-level index $H_2' = 0.46$ indicated intermediate specialisation once differences in marginal totals were standardised. Species overlap was low (Jaccard similarity = 0.17–0.36; Fig. 6); turnover accounted for 85 % of total beta diversity (*betapart*). For example, *Orchesia micans*, *Mycetophagus quadripustulatus* and *Triplax aenea* were strongly associated with *P. tremula*. Among red-listed taxa, *Dircaea australis* (VU) was primarily associated with *B. pubescens*, *Triplax rufipes* (NT) occurred mainly on *P. tremula*, and *Platyrhinus resinosus* (NT) was found only on *B. pubescens*. No single tree hosted all red-listed taxa, reinforcing the conservation importance of retaining mixed burned stands.

4. Discussion

Severe wildfire did not homogenise trunk-dwelling beetle assemblages across hosts. Instead, the present study suggests that tree species identity remained a dominant ecological filter for beetles, with high among-host turnover and widespread species-level preferences. By contrast, the broader arthropod assemblage exhibited only weak structuring according to tree host species, largely reflecting the abundance dynamics of Collembola (cf. Junggebauer et al., 2025). The persistence of host-structured beetle assemblages likely reflects tree-specific bark and wood traits—including bark thickness, fissuring, residual charcoal layers, moisture dynamics, and secondary chemistry—that govern fungal trajectories and microclimates of galleries and under-bark space. Such traits determine early saproxylic succession and the recruitment of both xylophages and mycetophages, consistent with experimental evidence that substrate type and tree identity shape saproxylic communities under non-fire mortality as well as after burns (e.g., Hägglund and Hjältén, 2018, Larsson Ekström et al., 2024). Hence, fire modifies but does not erase host filters.

The taxonomic composition observed in this burned forest ecosystem mirrors patterns documented in other forest microhabitat studies. Our evidence for strong beetle–tree host specificity persisting despite severe fire disturbance complements previous oak and pine studies showing similar patterns one to three years after low-severity burns (Fredriksson et al., 2020). Furthermore, the thickness of remaining bark, degree of fissuring, and extent of charcoal coating appear to influence beetle colonisation patterns, corroborating previous work on bark-related preferences (Brunet et al., 2010, Šebek et al., 2016). These parallel findings reinforce the principle that tree species identity remains a key driver of beetle—rather than all arthropod—community structure even following major disturbances (Seibold et al., 2015, Stokland and Meyke, 2008), carrying important implications for evidence-based conservation management.

Table 1

Results of multivariate generalised linear model (manyglm) examining differences in arthropod community composition between tree species. The model was fitted using a negative binomial distribution with tree species as the predictor variable and arthropod abundance as the response.

Contrast	Wald value	p-value
(Intercept)	273.15	0.001
Tree species: <i>P. sylvestris</i>	14.27	0.001
Tree species: <i>P. tremula</i>	18.30	0.001
Tree species: <i>Q. robur</i>	15.82	0.001

Table 2

Univariate test results for individual arthropod groups showing deviance (Dev) and adjusted p-values for tree species effects. Results are derived from negative binomial models with p-values adjusted for multiple comparisons. Only Collembola showed a statistically significant difference ($p < 0.05$) in abundance across tree species.

Arthropod group	Deviance	p-value
Collembola	44.382	0.049
Coleoptera	25.252	0.310
Oniscidea	18.160	0.439
Araneae	17.067	0.439
Aphidoidea	15.777	0.476
Diptera	14.082	0.605
Annelida	13.521	0.613
Hymenoptera	13.280	0.624
Chilopoda	12.791	0.624
Mixed	11.171	0.624
Diplopoda	9.147	0.624
Auchenorrhyncha	5.487	0.801
Gastropoda	5.564	0.801
Lepidoptera	5.285	0.801
Larvae	4.660	0.801
Neuroptera	4.340	0.801

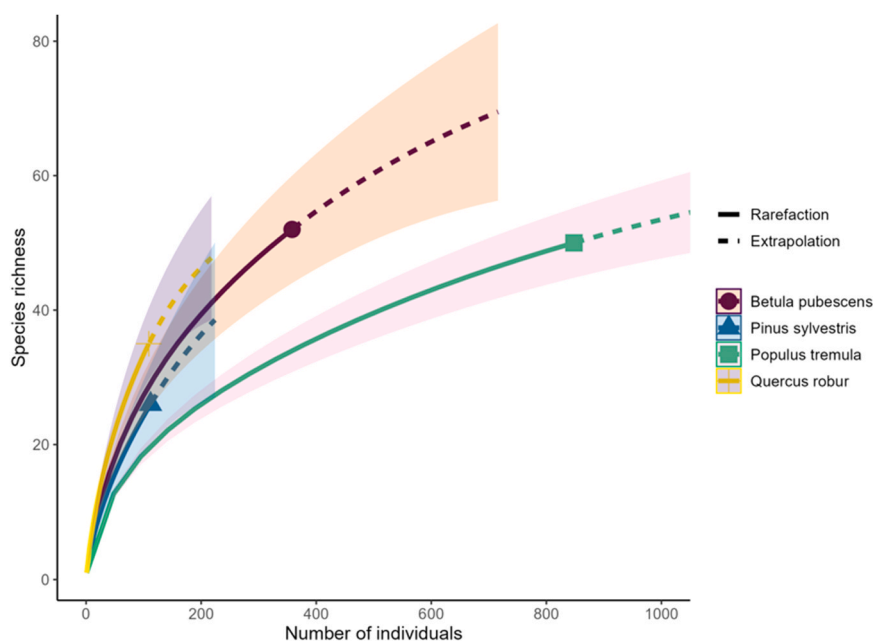


Fig. 3. Species accumulation curves for saproxylic beetle communities associated with four tree species. Rarefaction (solid lines) and extrapolation (dashed lines) curves show estimated species richness as a function of sampling effort (number of individuals). Points indicate the observed sample sizes and species richness for each tree species. Shaded areas represent 95 % confidence intervals. *Betula pubescens* (purple) shows the steepest accumulation curve and highest asymptotic richness estimate, while *P. tremula* (green) exhibits the flattest curve with the lowest projected species richness. *Pinus sylvestris* (blue) and *Q. robur* (yellow) show intermediate richness patterns. The wide confidence intervals, particularly for *P. sylvestris*, reflect uncertainty in extrapolation to larger sample sizes. Curves were generated using the iNEXT package with bootstrapping.

4.1. Host tree associations with arthropod communities

Although *P. tremula* supported higher overall arthropod abundance than *B. pubescens*, only Collembola showed significant variation at the assemblage level. This pattern suggests that microhabitat availability, possibly influenced by bark thickness and post-fire refuge conditions, can be more relevant than tree identity for some arthropod groups (Schowalter, 2012). Beetle communities, however, showed a markedly stronger association with tree species, explaining over 50 % of the variation in composition. The clear separation of *B. pubescens* and *P. sylvestris* in ordination space indicates that many saproxylic beetle species retain distinct host preferences, even in early post-fire conditions (Müller et al., 2015, Wu et al., 2008).

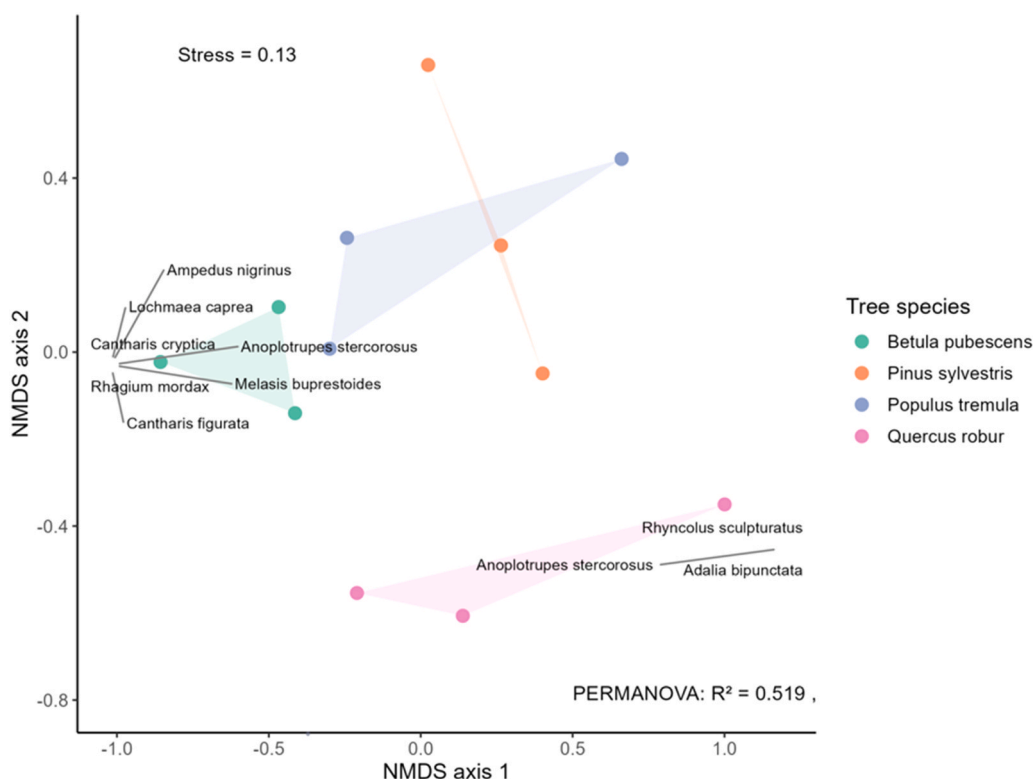


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of saproxylic beetle communities across four tree species. The ordination plot shows clear differentiation in beetle community composition among the four tree species (stress = 0.13). Each point represents a trap sample, with convex hulls (shaded areas) encompassing all samples from the same tree species. *Betula pubescens* (green) communities cluster in the negative region of axis 1, characterised by species such as *Rhagium mordax*, *Cantharis cryptica*, and *Ampedus nigrinus*. *Populus tremula* (blue) occupies the upper area of the ordination, while *P. sylvestris* (orange) shows greater dispersion along the first axis. *Quercus robur* (pink) forms a distinct cluster in the lower right quadrant, associated with species including *Adalia bipunctata* and *Rhyncolus sculpturatus*. PERMANOVA analysis confirmed that tree species identity explains 52 % of the variation in beetle community composition ($R^2 = 0.52$, $p = 0.002$).

4.2. Tree-specific beetle community patterns

Betula pubescens supported the highest beetle species richness, likely due to bark traits and decay processes that provide heterogeneous microhabitats (Milberg et al., 2014; Šebek et al., 2016). By contrast, *P. tremula* hosted fewer species but made up nearly 60 % of all beetle individuals collected, largely driven by aspen specialists attracted by wood-decaying fungi, such as *Orchesia micans* and *Triplax rufipes* (Sverdrup-Thygeson et al., 2010). *Pinus sylvestris* yielded the lowest beetle richness despite being as heavily burned and dead as the other tree species. This points to intrinsic host traits rather than vitality status. The thick, resin-rich bark and phloem, along with high lignin content, create a distinctive post-fire microenvironment that can delay fungal decay and constrain colonisation for many saproxylic taxa adapted to less resinous hosts. Resin compounds may persist after fire, modulate moisture and microbial activity, and thereby filter early colonists; comparable host-trait filters have been shown to shape post-disturbance saproxylic assemblages in other systems (Wikars, 2002). *Quercus robur* held intermediate richness but contributed unique species, consistent with oak's decay resistance and capacity to support specialised beetles in early post-fire stages (Parisi et al., 2019; Ulyshen and Sobotník, 2018). The non-asymptotic rarefaction curves (Fig. 3) for three of the four tree species suggest our sampling captured only a fraction of the actual beetle diversity. This under-sampling, particularly evident for *P. sylvestris*, introduces uncertainty into our species richness comparisons. However, such sampling limitation is a common challenge in post-disturbance studies of diverse arthropod communities (Martikainen and Kouki, 2003). Despite this constraint, the significant compositional differences detected among tree species indicate robust host specificity patterns transcending sampling limitations, suggesting our primary conclusions regarding beetle-tree associations remain valid. Nevertheless, future work would benefit from increased sampling intensity to better characterise the complete beetle assemblages associated with each tree species in post-fire environments.

Aspen specialists such as *O. micans* contribute to early wood-decay fungal dispersal, while *T. rufipes* feeds on polypore fruiting bodies and is considered fire-favoured in Fennoscandia. *Dicraea australis* is a fungivorous species developing in white-rotted deciduous wood colonised by *Trametes* fungi; its presence indicates rapid establishment of fungal substrates on sun-exposed birch snags after fire.

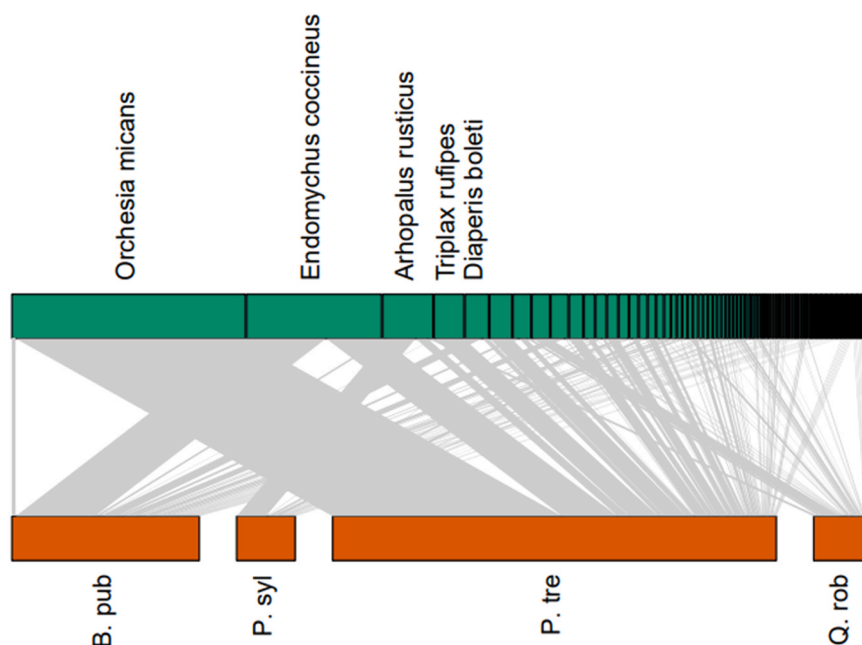


Fig. 5. Bipartite network visualisation of saproxylic beetle–tree host interactions. The network displays associations between beetle species (upper level, black bars) and host tree species (lower level, black bars). Line thickness represents the strength of association (abundance of beetles on each tree species), with thicker lines indicating higher abundances. Only a subset of beetle species names is displayed for clarity. The network illustrates moderate connectance (0.42), with most beetle species showing some degree of host preference while still maintaining connections across multiple tree species. *Betula pubescens* (B. pub) and *Populus tremula* (P. tre) support the largest number of beetle species, whereas *Pinus sylvestris* (P. syl) and *Quercus robur* (Q. rob) exhibit fewer but more specialised associations.

4.3. Species turnover and specialisation

Jaccard similarity indices (0.17–0.36) and beta diversity analyses both indicate substantial species turnover among the four tree species, rather than nestedness (Legendre, 2014). These findings highlight that each host contributes uniquely to overall beetle diversity, consistent with previous work demonstrating the complementary roles of multiple tree species for saproxylic assemblages (Lindenmayer et al., 2007). Red-listed taxa were similarly partitioned, with no single tree species supporting the full set of conservation-priority species (Hjältén et al., 2012). Bipartite network analysis revealed a relatively high level of specialisation (web asymmetry = 0.92), indicating that many species strongly associate with particular tree host species (Bascompte, 2009, Blüthgen et al., 2008, Dormann et al., 2017).

4.4. Comparison with living or unburned substrates

Comparable host-contingent responses to fire-altered substrates have been demonstrated experimentally for burned vs unburned spruce and birch logs, where fire exposure altered colonisation dynamics of wood-living insects (Wikars, 2002). Results from unburned Swedish mixed forests show lower dominance of aspen specialists and higher occupancy of shade-tolerant mycetophagids (Jonsson et al., 2016). Similarly, beetle communities on mechanically created (non-fire) snags exhibit greater nestedness and weaker host segregation (Hägglund and Hjältén, 2018, Wikars, 2002). These contrasts imply that wildfire not only increases dead-wood quantity but also intensifies host-specific filtering, perhaps through altered bark chemistry and moisture regimes.

4.5. Conservation and management implications

Retaining a diverse assemblage of burned trees appears pivotal for preserving saproxylic beetle diversity and associated ecosystem functions (Fischer et al., 2006, Swanson et al., 2011). We found *B. pubescens* and *P. tremula* to be especially important, with high beetle richness and abundance, respectively, yet all four studied tree species supported unique beetle taxa (Haack et al., 2022). Selective salvage logging that removes valuable trees such as pine, oak, and aspen, while leaving less preferred species may inadvertently reduce habitat availability for specialists, underscoring the need for management that retains high tree species richness (Kuuluvainen et al., 2019, Thorn et al., 2020). Integrating these insights into prescribed burning programmes and post-fire management can enhance both resilience and biodiversity conservation in boreal forests (Hekkala et al., 2016, Kelly et al., 2020).

Table 3

Host tree preferences and associated statistics for saproxylic beetles in a post-fire boreo-nemoral transition zone forest ecosystem. Data represent beetle-tree associations from trunk traps installed on four tree species in the Finsjöbrännan Nature Reserve. The table includes: scientific names of beetle species; total abundance across all sampled trees; preferred host tree species based on highest abundance; preference index (proportion of individuals found on the preferred host relative to the total abundance, with values from 0 to 1 where 1 indicates strict host specialisation); chi-square test statistics comparing observed distributions against random expectations; p-values indicating statistical significance of host preference; and conservation status according to the Swedish Red List (LC = Least Concern, NT = Near Threatened, VU = Vulnerable). NA statistically not evaluated due to low sample size.

Species	Total abundance	Host tree	Preference index	χ^2	P	Conservation status
<i>Dircaea australis</i>	11	<i>B. pubescens</i>	0.91	25.73	< 0.001	VU
<i>Prionychus melanarius</i>	7	<i>P. tremula</i>	0.86	14.14	0.003	VU
<i>Buprestis novemmaculata</i>	1	<i>P. sylvestris</i>	NA	NA	NA	VU
<i>Stenagostus rufus</i>	1	<i>P. sylvestris</i>	NA	NA	NA	VU
<i>Carphacus striatus</i>	1	<i>P. tremula</i>	NA	NA	NA	VU
<i>Ischnomera caerulea</i>	1	<i>P. tremula</i>	NA	NA	NA	VU
<i>Bostrichus capucinus</i>	1	<i>Q. robur</i>	NA	NA	NA	VU
<i>Triplax rufipes</i>	57	<i>P. tremula</i>	0.97	155.56	< 0.001	NT
<i>Platyrhinus resinosus</i>	9	<i>B. pubescens</i>	1	27	< 0.001	NT
<i>Xylotrechus antilope</i>	5	<i>Q. robur</i>	0.8	8.6	0.035	NT
<i>Peltis grossa</i>	1	<i>B. pubescens</i>	NA	NA	NA	NT
<i>Uloa culinaris</i>	1	<i>B. pubescens</i>	NA	NA	NA	NT
<i>Ips acuminatus</i>	1	<i>P. sylvestris</i>	NA	NA	NA	NT
<i>Orchesia micans</i>	446	<i>P. tremula</i>	0.98	1282.88	< 0.001	LC
<i>Endomychus coccineus</i>	258	<i>B. pubescens</i>	0.59	274.4	< 0.001	LC
<i>Arhopalus rusticus</i>	96	<i>P. sylvestris</i>	0.58	62.92	< 0.001	LC
<i>Diaperis boleti</i>	45	<i>B. pubescens</i>	0.73	64.6	< 0.001	LC
<i>Mycetophagus quadripustulatus</i>	42	<i>P. tremula</i>	1	126	< 0.001	LC
<i>Anaesthetis testacea</i>	34	<i>Q. robur</i>	0.97	94.24	< 0.001	LC
<i>Polydrusus cervinus</i>	34	<i>P. tremula</i>	0.41	8.82	0.032	LC
<i>Platystomos albinus</i>	33	<i>B. pubescens</i>	0.82	57.79	< 0.001	LC
<i>Rusticoclytus rusticus</i>	26	<i>P. tremula</i>	0.92	63.23	< 0.001	LC
<i>Triplax aenea</i>	20	<i>P. tremula</i>	1	60	< 0.001	LC
<i>Dorcus parallelepipedus</i>	20	<i>P. tremula</i>	0.6	14.8	0.002	LC
<i>Thanasimus femoralis</i>	20	<i>P. sylvestris</i>	0.35	2.8	0.423	LC
<i>Lygistopterus sanguineus</i>	18	<i>B. pubescens</i>	0.89	39.33	< 0.001	LC
<i>Tetratoma fungorum</i>	16	<i>P. tremula</i>	0.69	20.5	< 0.001	LC
<i>Ipidea binotata</i>	15	<i>P. sylvestris</i>	0.8	24.73	< 0.001	LC
<i>Triplax russica</i>	14	<i>P. tremula</i>	1	42	< 0.001	LC
<i>Aegomorphus clavipes</i>	13	<i>P. tremula</i>	0.46	7	0.072	LC
<i>Rhagium inquisitor</i>	8	<i>B. pubescens</i>	0.88	17	0.001	LC
<i>Tomoxia bucephala</i>	8	<i>P. tremula</i>	0.88	17	0.001	LC
<i>Thanasimus formicarius</i>	8	<i>Q. robur</i>	0.75	11	0.012	LC
<i>Hylobius abietis</i>	8	<i>P. sylvestris</i>	0.5	3	0.392	LC
<i>Pogonocherus decoratus</i>	7	<i>P. sylvestris</i>	0.57	7.29	0.063	LC
<i>Ampedus balteatus</i>	7	<i>B. pubescens</i>	0.43	3.86	0.277	LC
<i>Pissodes piniphilus</i>	6	<i>P. sylvestris</i>	0.83	11.33	0.01	LC
<i>Leptura quadrifasciata</i>	6	<i>B. pubescens</i>	0.5	6	0.112	LC
<i>Ampedus cinnabarinus</i>	6	<i>P. tremula</i>	0.5	3.33	0.343	LC
<i>Phymatodes testaceus</i>	5	<i>Q. robur</i>	1	15	0.002	LC
<i>Brachyderes incanus</i>	5	<i>P. sylvestris</i>	0.4	2.2	0.532	LC
<i>Prionychus ater</i>	5	<i>B. pubescens</i>	0.4	2.2	0.532	LC
<i>Spondylis buprestoides</i>	5	<i>Q. robur</i>	0.4	0.6	0.896	LC
<i>Bitoma crenata</i>	4	<i>B. pubescens</i>	1	12	0.007	LC
<i>Pyrochroa coccinea</i>	4	<i>B. pubescens</i>	1	12	0.007	LC
<i>Leiopus nebulosus</i>	4	<i>Q. robur</i>	1	12	0.007	LC
<i>Melanotus villosus</i>	4	<i>P. tremula</i>	0.5	4	0.261	LC
<i>Selatossomus aeneus</i>	4	<i>P. sylvestris</i>	0.5	2	0.572	LC
<i>Tasgius ater</i>	3	<i>B. pubescens</i>	1	9	0.029	LC
<i>Cantharis livida</i>	3	<i>P. tremula</i>	1	9	0.029	LC
<i>Dromius angustus</i>	3	<i>B. pubescens</i>	0.67	3.67	0.3	LC
<i>Chrysanthia geniculata</i>	3	<i>P. tremula</i>	0.67	3.67	0.3	LC
<i>Stictoleptura rubra</i>	3	<i>P. tremula</i>	0.67	3.67	0.3	LC
<i>Hylobius pinastri</i>	3	<i>B. pubescens</i>	0.33	1	0.801	LC
<i>Dromius agilis</i>	3	<i>P. sylvestris</i>	0.33	1	0.801	LC
<i>Anoplotrupes stercorosus</i>	2	<i>Q. robur</i>	NA	NA	NA	LC
<i>Cantharis cryptica</i>	2	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Melasis buprestoides</i>	2	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Rhagium mordax</i>	2	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Trixagus dermestoides</i>	2	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Ampedus sanguineus</i>	2	<i>P. sylvestris</i>	NA	NA	NA	LC

(continued on next page)

Table 3 (continued)

Species	Total abundance	Host tree	Preference index	χ^2	P	Conservation status
<i>Ampedus pomorum</i>	2	<i>P. tremula</i>	NA	NA	NA	LC
<i>Chrysomela populi</i>	2	<i>P. tremula</i>	NA	NA	NA	LC
<i>Poecilium albi</i>	2	<i>Q. robur</i>	NA	NA	NA	LC
<i>Cis boleti</i>	2	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Hemicrepidius hirtus</i>	2	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Chrysanthia viridissima</i>	2	<i>P. sylvestris</i>	NA	NA	NA	LC
<i>Paraphotistus impressus</i>	2	<i>P. sylvestris</i>	NA	NA	NA	LC
<i>Pissodes pini</i>	2	<i>P. sylvestris</i>	NA	NA	NA	LC
<i>Ampedus nigrinus</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Anisotoma glabra</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Aplocnemus impressus</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Cantharis figurata</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Dacne bipustulata</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Dasytes niger</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Hylis olexai</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Lochmaea caprea</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Magdalis frontalis</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Myrrha octodecimguttata</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Strophosoma melanogrammum</i>	1	<i>B. pubescens</i>	NA	NA	NA	LC
<i>Aplocnemus nigricornis</i>	1	<i>P. sylvestris</i>	NA	NA	NA	LC
<i>Ocypus brunneipes</i>	1	<i>P. sylvestris</i>	NA	NA	NA	LC
<i>Astenus lyonesius</i>	1	<i>P. tremula</i>	NA	NA	NA	LC
<i>Globicornis emarginata</i>	1	<i>P. tremula</i>	NA	NA	NA	LC
<i>Hypoganus inunctus</i>	1	<i>P. tremula</i>	NA	NA	NA	LC
<i>Lordithon lunulatus</i>	1	<i>P. tremula</i>	NA	NA	NA	LC
<i>Thymalus limbatus</i>	1	<i>P. tremula</i>	NA	NA	NA	LC
<i>Adalia bipunctata</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Cantharis nigra</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Coccinella septempunctata</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Cryptophagus scanicus</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Curculio venosus</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Rhyncolus sculpturatus</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Saperda scalaris</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Scolytus ratzeburgi</i>	1	<i>Q. robur</i>	NA	NA	NA	LC
<i>Sericus brunneus</i>	1	<i>Q. robur</i>	NA	NA	NA	LC

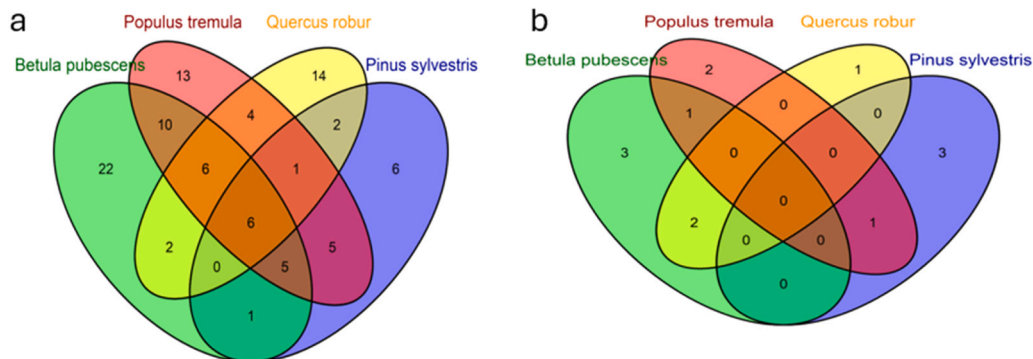


Fig. 6. Venn diagrams showing beetle species distribution across four tree species in a post-fire boreo-nemoral transition zone forest (a) Distribution of all recorded beetle species ($n = 96$) across the four tree species, illustrating the number of species unique to each tree host and the degree of community overlap. Numbers in each segment represent beetle species count (b) Distribution of red-listed beetle species across the four tree hosts, highlighting the conservation value of different tree species. This visualisation demonstrates both host specialisation patterns and the complementary role of other tree species in supporting beetle diversity, particularly for species of conservation concern.

4.6. Future research directions

Future studies should span extended post-fire chrono sequences under varying burn severities, including unburned reference sites, to clarify long-term succession dynamics (e.g., Forsman et al., 2011). Experimental work on how dead-wood density and volatile organic compounds shape beetle host selection would also deepen the understanding of saproxylic habitat requirements (Heikkala et al., 2016). Tracking both specialist and generalist species in protected and managed stands will be crucial for adaptive conservation planning as fire regimes evolve.

5. Conclusions

Our results demonstrate that fire does not homogenise beetle assemblages but instead highlight specialised tree–beetle relationships. Variation in beetle community composition among tree host species, combined with the uneven distribution of red-listed beetles, highlights the importance of maintaining diverse post-fire tree assemblages. Given that climate change is projected to intensify fire regimes (McLauchlan et al., 2020), retaining mixed-species stands is essential for safeguarding the long-term persistence of saproxylic insects and, by extension, the broader forest biodiversity (Wright and Bailey, 1982).

CRedit authorship contribution statement

Anders Forsman: Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition. **Markus Franzén:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Olof Persson:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

We have nothing to declare.

Acknowledgements

We thank Jonas Lundqvist (Vetlanda) for invaluable field assistance and for verifying the identification of beetle species. We are also grateful to the provincial government of Kalmar, which surveyed the area in 2022. Jesper Hansson protected and rescued the site from intense forestry practices.

Data availability

Data will be made available on request.

References

- Agency, S.E.P., 2020. Nationella marktäckedata 2018 basskikt: Produktbeskrivning [National Land-Cover Data 2018 Basic Layer: Product Description]. Version 2.2; 7 July 2020. Swedish Environmental Protection Agency, Stockholm.
- Bascompte, J., 2009. Disentangling the web of life. *Science* 325, 416–419.
- Baselga, A., Orme, C.D.L., 2012. betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* 3, 808–812.
- Blüthgen, N., Fründ, J., Vázquez, D.P., Menzel, F., 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89, 3387–3399.
- Bond, W.J., Keeley, J.E., 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* 20, 387–394.
- Brin, A., Bouget, C., 2018. Biotic interactions between saproxylic insect species. In: Ulyshen, M. (Ed.), *Saproxylic insects: diversity, ecology and conservation*. Springer, Heidelberg, pp. 471–514.
- Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests—a review with recommendations for sustainable forest management. *Ecol. Bull.* 77–94.
- Certini, G., 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143, 1–10.
- Chen, H., Boutros, P.C., 2011. VennDiagram: a package for the generation of highly-customizable Venn and Euler diagrams in R. *BMC Bioinforma.* 12, 1–7.
- Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: analysing ecological networks. *R. N.* 8, 8–11.
- Dormann, C.F., Fründ, J., Schaefer, H.M., 2017. Identifying causes of patterns in ecological networks: opportunities and limitations. *Annu. Rev. Ecol. Evol. Syst.* 48, 559–584.
- Eide, W., Ahnén, K., Bjelke, U., Nordström, S., Ottosson, E., Sandström, J., Sundberg, S., 2020. Tillstånd och trender för arter och deras livsmiljöer - rödlistade arter i Sverige 2020. Artdatabanken, SLU, Uppsala.
- Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Front. Ecol. Environ.* 4, 80–86.
- Flannigan, M., Bergeron, Y., Engelmark, O., Wotton, B., 1998. Future wildfire in circumboreal forests in relation to global warming. *J. Veg. Sci.* 9, 469–476.
- Forsman, A., Karlsson, M., Wennersten, L., Johansson, J., Karpestam, E., 2011. Rapid evolution of fire melanism in replicated populations of pygmy grasshoppers. *Evolution* 65, 2530–2540.
- Fredriksson, E., Mugerwa Pettersson, R., Naalisvaara, J., Löfroth, T., 2020. Wildfire yields a distinct turnover of the beetle community in a semi-natural pine forest in northern Sweden. *Ecol. Process.* 9, 44.
- de Groot, W.J., Flannigan, M.D., Cantin, A.S., 2013. Climate change impacts on future boreal fire regimes. *For. Ecol. Manag.* 294, 35–44.
- Haack, N., Borges, P.A., Grimm-Seyfarth, A., Schlegel, M., Wirth, C., Bernhard, D., Brunk, I., Henle, K., Pereira, H.M., 2022. Response of common and rare beetle species to tree species and vertical stratification in a floodplain forest. *Insects* 13, 161.
- Hägglund, R., Hjaltn, J., 2018. Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides. *For. Ecol. Manag.* 425, 45–58.
- Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S., Kouki, J., 2016. Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. *For. Ecol. Manag.* 359, 51–58.
- Hekkala, A.-M., Ahtikoski, A., Pääta, M.-L., Tarvainen, O., Siipilehto, J., Tolvanen, A., 2016. Restoring volume, diversity and continuity of deadwood in boreal forests. *Biodivers. Conserv.* 25, 1107–1132.
- Hjaltn, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P., Hilszczański, J., 2012. Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. *PLoS One* 7, e41100.
- Hsieh, T., Ma, K., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451–1456.
- Johansson, N., 2024. Review of the Swedish Species of *Lissonota* Gravenhorst: (Hymenoptera: Ichneumonidae: Banchinae) with an Illustrated Key to the Females of the Western Palaearctic. Sver. Entomol. F. örening.
- Jonsson, B.G., Ekström, M., Esseen, P.-A., Grafström, A., Ståhl, G., Westerlund, B., 2016. Dead wood availability in managed Swedish forests—Policy outcomes and implications for biodiversity. *For. Ecol. Manag.* 376, 174–182.

- Junggebauer, A., Jüds, M., Salamon, J.-A., Pollierer, M.M., Scheu, S., 2025. Temporal dynamics and stability of Collembola communities in Central European forests: the roles of forest management, climate and regional factors. *For. Ecol. Manag.* 598, 123239.
- Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., Bennett, A.F., Buckland, S.T., Canelles, Q., Clarke, M.F., 2020. Fire and biodiversity in the Anthropocene. *Science* 370, eabb0355.
- Kuuluvainen, T., Lindberg, H., Vanha-Majamaa, I., Keto-Tokoi, P., Punttila, P., 2019. Low-level retention forestry, certification, and biodiversity: case Finland. *Ecol. Process.* 8, 1–13.
- Larsson Ekström, A., Djupström, L.B., Hjältén, J., Sjögren, J., Jönsson, M., Löfroth, T., 2024. Deadwood manipulation and type determine assemblage composition of saproxylic beetles and fungi after a decade. *J. Environ. Manag.* 372, 123416.
- Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. *Glob. Ecol. Biogeogr.* 23, 1324–1334.
- Lindenmayer, D., Fischer, J., Felton, A., Montague-Drake, R., D. Manning, A., Simberloff, D., Youngentob, K., Saunders, D., Wilson, D., M. Felton, A., 2007. The complementarity of single-species and ecosystem-oriented research in conservation research. *Oikos* 116, 1220–1226.
- Martikainen, P., Kouki, J., 2003. Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodivers. Conserv.* 12, 1815–1831.
- McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., 2020. Fire as a fundamental ecological process: Research advances and frontiers. *J. Ecol.* 108, 2047–2069.
- Milberg, P., Bergman, K.O., Johansson, H., Jansson, N., 2014. Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. *Insect Conserv. Divers.* 7, 508–522.
- Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., Gossner, M.M., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. *J. Appl. Ecol.* 52, 753–762.
- Nilsson, M., Ahlkrona, E., Jönsson, C., Allard, A., 2020. Regionala jämförelser mellan Nationella Marktäckedata och fältdata från Riksskogstaxeringen och NILS. Naturvårdsverket, Stockholm.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan: community ecology package*. R package. *vegan: Community Ecology Package*.
- Parisi, F., Di Febbraro, M., Lombardi, F., Biscaccianti, A., Campanaro, A., Tognetti, R., Marchetti, M., 2019. Relationships between stand structural attributes and saproxylic beetle abundance in a Mediterranean broadleaved mixed forest. *For. Ecol. Manag.* 432, 957–966.
- Saint-Germain, M., Drapeau, P., Hébert, C., 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. *Biol. Conserv.* 118, 583–592.
- Schimmel, J., Granström, A., 1996. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77, 1436–1450.
- Schowalter, T., 2012. Insect responses to major landscape-level disturbance. *Annu. Rev. Entomol.* 57, 1–20.
- Sebek, P., Vodka, S., Bogusch, P., Pech, P., Tropek, R., Weiss, M., Zimova, K., Čížek, L., 2016. Open-grown trees as key habitats for arthropods in temperate woodlands: the diversity, composition, and conservation value of associated communities. *For. Ecol. Manag.* 380, 172–181.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol.* 29, 382–390.
- Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., Boulanger, Y., Burton, P.J., De Grandpré, L., Gauthier, S., 2020. Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. *Ecography* 43, 967–978.
- Stokland, J.N., Meyke, E., 2008. The saproxylic database: an emerging overview of the biological diversity in dead wood. *Rev. D. Écologie (La Terre Et. la Vie)* 63, 37–48.
- Sverdrup-Thygeson, A., Skarpaas, O., Ødegaard, F., 2010. Hollow oaks and beetle conservation: the significance of the surroundings. *Biodivers. Conserv.* 19, 837–852.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Front. Ecol. Environ.* 9, 117–125.
- Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T.P., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. *Nat. Commun.* 11, 4762.
- Ulyshen, M.D., Sobotnik, J., 2018. An introduction to the diversity, ecology, and conservation of saproxylic insects. In: Ulyshen, M.D. (Ed.), *Saproxylic insects: diversity, ecology and conservation*. Springer, Cham, pp. 1–47.
- Wang, Y., Naumann, U., Wright, S.T., Warton, D.I., 2012. mvabund—an R package for model-based analysis of multivariate abundance data. *Methods Ecol. Evol.* 3, 471–474.
- Weisser, W.W., Siemann, E., 2004. *Insects and Ecosystem Function*. Ecological Studies. Springer, Heidelberg.
- Wikars, L.-O., 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. *J. Insect Conserv.* 6, 1–12.
- Wright, H.A., Bailey, A.W., 1982. *Fire Ecology: United States and Southern Canada*. John Wiley & Sons, New York.
- Wu, J., Yu, X.D., Zhou, H.Z., 2008. The saproxylic beetle assemblage associated with different host trees in Southwest China. *Insect Sci.* 15, 251–261.