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# Forest management history, habitat heterogeneity, and landscape context shape parasitoid wasp (Ichneumonoidea) abundance in boreal spruce forests

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## Abstract

Forest management history can alter forest structure and landscape configuration in ways that affect insect communities, yet responses of parasitoid wasps to these changes remain poorly understood. We compared near-natural forests with mature formerly clear-cut forests to investigate how forest management history and environmental variables influence the abundance of parasitoid wasps (Ichneumonoidea) in spruce-dominated boreal forests of southeastern Norway. Parasitoid wasps were sampled using Malaise traps across twelve paired locations and identified to subfamily level. Abundance was analysed in relation to forest management type, dead wood characteristics, habitat connectivity at local (0.5 km) and regional (20 km) scales, and climatic variables. Near-natural forests supported higher abundances of Ichneumonidae, Ichneumoninae, and both generalist and saproxylic parasitoid wasps, whereas formerly clear-cut forests supported higher abundance of Tryphoninae. Dead wood diversity was positively associated with multiple taxa and functional groups, whereas dead wood volume had no effect, highlighting the importance of heterogeneity in dead wood resources. Connectivity effects were taxon- and scale-dependent: Tryphoninae responded negatively to local connectivity, while Cryptinae and saproxylic parasitoid wasps responded positively to regional connectivity. Temperature was negatively associated with several parasitoid wasp groups, whereas precipitation showed no detectable effects. Overall, parasitoid wasp abundance reflected taxon-specific and scale-dependent responses to forest structure and landscape context.

**Implications for insect conservation**: Retaining near-natural forest conditions, promoting diverse dead wood structures, and maintaining regional connectivity of old spruce forests may help sustain parasitoid wasp populations and the ecological functions they provide in boreal forest ecosystems.

## Introduction

Industrial forest management, driven primarily by demand for timber and pulp, has fundamentally altered boreal forests, resulting in long-term structural simplification and biodiversity decline (Esseen et al. 1997; Lunde et al. 2025; Siitonen 2001). Insects are major components of forest biodiversity (Hébert 2023; Wermelinger 2021; Wermelinger et al. 2013), and accumulating evidence from several regions indicates negative trends across multiple insect biodiversity metrics, although patterns vary among ecosystems and taxa (Seibold et al. 2019; Wagner 2020). Despite this, the effects of forestry on the hyperdiverse and taxonomically challenging order of Hymenoptera remain largely unknown (Forbes et al. 2018; Lunde et al. 2025).

Parasitoid wasps (Hymenoptera: Ichneumonoidea) are important regulators of other arthropods, with larvae that develop by feeding on and ultimately killing their hosts (Godfray 1994; Gullan and Cranston 2014; Hilszczański 2018; Quicke 2015). As a highly speciose and ecologically influential insect group (Forbes et al. 2018; Gaston 1991; Quicke 2015), they play a key regulatory role in forest ecosystems by reducing populations of bark beetles and other insects (Hilszczański 2018; Kenis and Hilszczanski 2004). Their functional importance makes it necessary to better understand their ecology, including how they respond to forest management.

Understanding these dynamics is particularly critical in Norway, where forests host over half of all described species, including 48% of those listed as threatened on the Norwegian Red List for Species (Artsdatabanken 2021b; Framstad et al. 2018). Notably, as many as 84% of the threatened forest species are assumed to be associated with old-growth forest characteristics (Artsdatabanken 2021b), highlighting the conservation importance of structurally complex and long-continuity forest habitats.

Since the mid-20th century, clear-cutting, defined as the practice of harvesting most or all trees from a stand, has become the dominant forest management method in Norway (Seedre et al. 2018; Storaunet and Rolstad 2020; Storaunet et al. 2005). By 2016, only 30% of all productive forests in Norway had not undergone clear-cutting (Storaunet and Rolstad 2020).

Clear-cutting with single-species tree planting produces even-aged stands with low structural complexity and limited dead wood, particularly of large dimensions, because early harvesting interrupts natural mortality cycles (Asplund et al. 2024; Kuuluvainen et al. 2012; Siitonen 2001; Storaunet et al. 2005). At the landscape scale, the extent and spatial configuration of clear-cuts can reduce connectivity of old-growth-associated forest habitat, limiting persistence and recolonization for species adapted to stable, long-continuity forest environments (Asplund et al. 2024; Komonen et al. 2000; Lunde et al. 2025). Prior to the onset of clear-cutting, selective logging methods based on preferred tree diameters were more commonly practised (Storaunet and Rolstad 2020; Storaunet et al. 2005). Such forests often developed characteristics similar to old-growth forests, including heterogeneous structure, multi-layered canopies, and greater volumes of dead wood (Jacobsen et al. 2020; Siitonen 2001; Siitonen et al. 2000; Storaunet and Rolstad 2020; Storaunet et al. 2005).

Dead wood is a key structural component that supports biodiversity in boreal forests (Stokland et al. 2012; Storaunet et al. 2005; Ulyshen and Šobotník 2018). A wide range of organisms, including fungi, insects, birds, and mammals, depend on dead or dying wood for food, shelter, or reproduction, and are collectively termed saproxylic (Speight 1989; Stokland et al. 2012; Ulyshen and Šobotník 2018). Saproxylic insects may comprise as much as 20–30% of the forest insect fauna in northern Europe (Ulyshen and Šobotník 2018). Among these are numerous parasitoid wasps, such as those in the superfamily Ichneumonoidea, that parasitize larvae of wood-associated hosts (Broad et al. 2018; Hilszczański 2018; Quicke 2015).

Parasitoid wasps can live outside or inside their hosts. Those living on the outside (ectoparasitoids) usually prevent host development by immediately paralyzing or killing the host after parasitism, a strategy grouping them as idiobionts (Askew and Shaw 1986; Broad et al. 2018; Haeselbarth 1978a; Haeselbarth 1978b; Hilszczański 2018; Quicke 2015). They are typically generalists, as they do not need to overcome internal host immune defences (Broad et al. 2018; Godfray 1994; Hilszczański 2018; Quicke 2015). Those parasitoids living inside their hosts (endoparasitoids), however, usually allow their hosts to continue development after parasitism, a strategy grouping them as koinobionts. Some koinobionts may even manipulate their host's growth physiology, resulting in a delay in host maturation (Godfray 1994; Hilszczański 2018). These species are often host-specific due to the need to overcome host immune defences (Broad et al. 2018; Godfray 1994; Hilszczański 2018; Quicke 2015). Although these associations are not absolute, as some ectoparasitoids are koinobionts and some endoparasitoids are idiobionts (Broad et al. 2018; Quicke 2015; Shaw 2006), they broadly describe the main life-history strategies of parasitoid wasps, particularly the saproxylic ones (Hilszczański 2018).

Specialist species are generally more vulnerable to extinction than generalists, owing to their narrower ecological niches and limited dietary or habitat flexibility (Clavel et al. 2011; Dennis et al. 2011; McKinney 1997). Extinction risk also tends to increase with trophic level (McKinney 1997; Purvis et al. 2000). Thus, it would be expected that parasitoid wasps struggle in boreal forests as they inhabit high positions in trophic food chains, and that specialists like koinobionts may be more sensitive to the quality and continuity of forests than their hosts (Hilszczański 2018; Shaw and Hochberg 2001).

In Finland, Komonen et al. (2000) found that in landscapes with a history of clear-cutting, species across the wood-decay food chain declined, with the strongest losses occurring among higher-trophic, specialized taxa. In Sweden, Hilszczański et al. (2005) reported that forest management type and dead wood characteristics significantly influenced parasitoid wasp assemblages associated with saproxylic beetles. Koinobionts were less abundant in recent clear-cuts compared to old-growth and mature managed forests, whereas idiobionts showed the opposite pattern. This trend was further supported by Stenbacka et al. (2010) who found idiobionts to be more abundant in recent clear-cuts, while koinobionts were more abundant in mature managed and old-growth forests. To our knowledge, the long-term effects of clear-cutting on parasitoid wasps remain largely unexplored.

To further explore these patterns, we examined how structural habitat features such as dead wood volume and diversity influence parasitoid wasp abundance, alongside other environmental variables including temperature, precipitation, and habitat connectivity at local and regional scales. Structural features like dead wood, particularly its volume and diversity, provide critical habitat and host resources for saproxylic insects (Hilszczański 2018; Hottola et al. 2009; Norkute et al. 2025; Stokland et al. 2012; Ulyshen and Šobotník 2018). Microclimatic conditions, including temperature and precipitation, can shape insect activity, development rates, and host-parasitoid interactions (Deutsch et al. 2008; Forrest 2016; Hance et al. 2007; Shapiro and Pickering 2000). Additionally, habitat connectivity may influence the ability of parasitoids to disperse into and colonize suitable habitat, particularly for species with limited mobility or specialized habitat requirements (Bengtsson et al. 2000; Cronin and Reeve 2005; Jonsell et al. 1999). Despite their potential importance, these variables are rarely examined in combination with forest management effects on parasitoid wasps.

The status and ecology of parasitoid wasps in Norway, particularly those in the superfamily Ichneumonoidea, remain poorly understood (Artsdatabanken 2021a; Ødegaard et al. 2021). Given their importance as regulators of other arthropods within forest ecosystems (Hilszczański 2018; Kenis and Hilszczanski 2004), and the evidence that certain groups may be especially vulnerable to forestry practices (Hilszczański et al. 2005; Komonen et al. 2000; Stenbacka et al. 2010), it is important to understand how long-term forest management affects this ecologically diverse group.

The aim of this study was to compare near-natural forests, i.e. forests that have never been clear-cut, with mature formerly clear-cut forests to assess the long-term effects of forest management on the abundance within Ichneumonoidea families and subfamilies in spruce-dominated forests in southeastern Norway. Specifically, we asked:

1. 1. Are there differences in abundance within Ichneumonoidea families and subfamilies between near-natural and formerly clear-cut forests?
2. 2. Are there differences in the abundance of generalist (idiobiont) and specialist (koinobiont) Ichneumonoidea between the two forest management types?
3. 3. Do near-natural and formerly clear-cut forests differ in the abundance of saproxylic Ichneumonoidea?
4. 4. To what extent do local and regional environmental variables drive differences in Ichneumonoidea abundance?

## Materials and Methods

# Study area and design

This study is part of the EcoForest project, focusing on the long-term effects of clear-cutting forestry on biodiversity, carbon storage and functions in boreal forests. The project compares mature forests with a history of clear-cutting (CC) with near-natural forests that have never been clear-cut (NN). The near-natural forests have been selectively cut in the past, while the clear-cut forests were cut in the 1940s–1960s (Asplund et al. 2024).

Twelve locations in southeastern Norway were surveyed (Fig. 1), each with two sites (CC and NN) of boreal forest dominated by Norway spruce (*Picea abies* (L.) H. Karst.), separated by no more than 5 km (Asplund et al. 2024). The site pairs had similar soil type, bedrock, slope, aspect, productivity, and elevation. The elevation between locations ranged from 178 to 668 meters above sea level (MASL), with an average of 452 MASL across all sites. None of the sites showed signs of fertilisation, commercial thinning, drainage, or bark beetle (*Ips typographus*) attacks, and the near-natural sites were without signs of recent human activity or dead wood removal (Asplund et al. 2024).

## Insect trapping

Insects from locations 1–10 were collected in 2022, while those from locations 11 and 12 were collected in 2023 (Fig. 1). The insects were collected with black and white Malaise traps (BugDorm, Taiwan) fastened to a living tree (Fig. 2).

Each site was represented by two traps: one placed to the north, and one placed to the south of a central 15 x 15 m plot. The collection bottles were filled with 96% ethanol and wrapped in aluminium foil in order to avoid DNA degradation, as the insect communities would also be identified by DNA as part of another study.

The traps were activated at the end of May and emptied every second week until the end of July, giving a total trapping period of two months. The insects were transferred to a -20°C freezer before undergoing DNA extraction through a lysis process. After lysis, the Malaise trap bottles were emptied through a fine sieve, separating the insects from the lysis solution. The insects were subsequently placed in a petri dish with 85% ethanol for identification.

## Insect sorting and identification

Due to a high workload, we sorted insects only from the traps placed to the north and from two collection periods (1 and 3). Period 1 corresponds to the first half of June, and period 3 to the first half of July. We used a stereo microscope to sort all insects into orders and to identify families and subfamilies within the superfamily Ichneumonoidea. Identification of families of Ichneumonoidea and subfamilies of Ichneumonidae followed Broad et al. (2018). For the identification of Braconidae subfamilies, we used Goulet and Huber (1993), Nastasi et al. (2024), and “Mike’s Insect Keys” (Hackston 2024). We also consulted an unpublished identification guide (Karlsson 2005, booklet from the Swedish Malaise Trap Project). Identification of Ichneumonoidea was carried out by experts (Alf Tore Mjøs and Jarl Birkeland), in collaboration with the first author.

Subfamilies were annotated as generalist (idiobiont) or specialist (koinobiont) based on Broad et al. (2018), Jasso-Martínez et al. (2022), and Quicke (2015). Saproxylicity was annotated following Hilszczański (2018), supplemented with host information from Broad et al. (2018) and Quicke (2015). All additional sources used for these annotations are listed in Appendix S1 of Online Resource 1. “Saproxylic” and “partly saproxylic” categories were combined due to the limited number of “fully saproxylic” subfamilies in our samples. No information was found on the saproxylicity of the subfamily Brachistinae, which has undergone several recent revisions. Brachistinae includes several tribes formerly placed in Helconinae, as well as other tribes formerly in other subfamilies (Chen and van Achterberg 2019; Sharanowski et al. 2011). Since Helconinae is considered saproxylic by Hilszczański (2018), we annotated Brachistinae as saproxylic as well. It is important to note that research on the phylogeny of this group is ongoing, with multiple sources presenting differing views (Chen and van Achterberg 2019; Jasso-Martínez et al. 2022; Quicke 2015; Sharanowski et al. 2011). The life history of Telengaiinae (formerly Gnamptodontinae) remains uncertain, with early works suggesting koinobiont endoparasitoids (Belshaw et al. 2003; Shaw and Huddleston 1991) and Quicke (2015) emphasizing the overall lack of biological knowledge, whereas more recent sources infer idiobiont ectoparasitoids based on phylogeny (Chen and van Achterberg 2019; Jasso-Martínez et al. 2022). We therefore treat Telengaiinae as idiobionts in our analyses. Phygadeuontinae are generally considered idiobiont ectoparasitoids, although exceptions may occur (Broad et al. 2018). Owing to limited literature and time constraints, all Phygadeuontinae in our study were treated as idiobiont.

## Environmental variables

Dead wood volume ($m^3ha^{-1}$) was calculated from measurements collected in a 133.33 x 15 m transect with the 15 x 15 m plot at its centre (Asplund et al. 2024). All standing and downed dead wood originating inside the transect with a diameter at breast height or basal diameter of ≥ 5 cm was measured (Asplund et al. 2024). Total dead wood volume (standing + downed) was included as an environmental variable in our analyses. Dead wood measurements and calculation procedures follow Asplund et al. (2024).

Dead wood diversity was quantified using the W(x, y) index developed by Hottola et al. (2009), which integrates both the amount and heterogeneity of dead wood resources. The metric is based on the quantity of different dead wood types defined by tree species, decay class, position (standing or downed), and size class. Values were calculated from the dead wood inventory data of Asplund et al. (2024) following the implementation described by Norkute et al. (2025), using parameter settings of x = 1.39 and y = 0.25.

Air temperature (°C) was recorded every 15 minutes using TMS-4 data loggers (TOMST s.r.o., Prague, Czech Republic) installed 15 cm above the ground in the main plot, following the field setup described in Asplund et al. (2024). Logger specifications are described in Wild et al. (2019). The

mean temperature for each site was calculated over the sampling season, from the date of trap activation (22 May 2022 and 26 May 2023) until removal (27 July 2022 and 27 July 2023).

Precipitation (mm/day) was obtained from the seNorge2018 dataset provided by the Norwegian Meteorological Institute (MET Norway n.d.) through their THREDDS server. For each site, we calculated the mean of daily total precipitation over the sampling season, using data from 2022 and 2023.

Connectivity of old spruce forests, defined as how connected the sites are to old forest habitat, was calculated as the sum of living spruce volume ($m^3ha^{-1}$) from forest stands above 80 years old within a 25 km radius from the main plot, assuming mean dispersal distances of 0.5 km (local) and 20 km (regional) (Asplund et al. 2024).

# Data analysis

We created all figures and performed statistical analyses using the software environment R version 4.3.3 (R Core Team 2024) and RStudio version 2024.09.0 + 375 (Posit Team 2024). To visualize differences in taxonomic abundance between NN and CC, we used the metacoder package version 0.3.9 (Foster et al. 2017). Phylogenetic structure followed Broad et al. (2018) for Ichneumonidae and Jasso-Martínez et al. (2022) for Braconidae. Taxonomic data were parsed into a hierarchical format using the $parse_taxa_data()$ function, and individual counts were aggregated by taxon. Differences in taxon abundance between NN and CC were assessed using Wilcoxon rank-sum test (Wilcoxon 1945) via the $compare_groups()$ function. To visualize the results, we generated a heat tree.

Data exploration followed the protocol of Zuur et al. (2010). We examined 13 response variables representing different levels of taxonomic and ecological resolution: the two Ichneumonoid families (Ichneumonidae and Braconidae), eight subfamilies with more than 100 individuals, generalist and specialist Ichneumonoidea, and saproxylic Ichneumonoidea (Appendix S2 of Online Resource 1). All response variables significantly deviated from normality (Shapiro-Wilk test for normality: $p < 0.05$), indicating that standard linear models assuming normality were not appropriate. Consequently, we analysed the data using generalized linear mixed models (GLMMs), which incorporate both fixed and random effects and are suitable for non-normal response data (Bolker et al. 2009). To avoid pseudoreplication, we accounted for the variation between the different sites by setting site as a random effect (Bolker et al. 2009; Harrison et al. 2018).

We used the glmmTMB package version 1.1.9 (Brooks et al. 2017) to fit GLMMs. We initially fitted all GLMMs with a Poisson distribution, which is commonly used for modelling count data in ecology (Bolker et al. 2009; Hilbe 2011). We assessed model fit using simulation-based diagnostics from the DHARMa package version 0.4.7 (Hartig 2024). If these diagnostics indicated significant overdispersion or quantile deviations, models were refitted using a negative binomial distribution to better account for variance structure (Harrison 2014; Hilbe 2011). Only models for which DHARMa explicitly reported “no significant problems detected” were retained in the Poisson form to ensure conservative model adequacy. This two-step approach reflects standard practice in ecological modelling when addressing overdispersion in ecological count data (Richards 2008).

We standardized all continuous predictor variables (dead wood volume, dead wood diversity, mean temperature, mean precipitation, local connectivity at 0.5 km, and regional connectivity at 20 km) using the $sca \leq ()$ function in R (Becker et al. 1988). This applies a z-score transformation, resulting in variables with a mean of 0 and a variance of 1 (Milligan and Cooper 1988). Standardization was performed to set the variables on a similar, comparable scale (Grueber et al. 2011; Milligan and Cooper 1988) and to resolve convergence issues we encountered during model fitting.

To address potential correlations among predictor variables, we calculated pairwise Pearson and Spearman correlation coefficients between the standardized continuous predictors. A conservative threshold of $|r| > 0.5$ was used to flag moderate to strong correlations (Mukaka 2012). Correlated pairs (Appendix S3 of Online Resource 1) were not included in the same candidate models to avoid instability in parameter estimates (James et al. 2021).

Candidate models were specified *a priori* based on ecological knowledge about the relevance of each predictor to the response variables (Appendix S4 of Online Resource 1). All candidate models were tested across the full set of response variables defined earlier. The variable “year” was included in all models to control for temporal variation, as some sites were sampled in different years. The first candidate model fitted only the predictor “forest type” (representing NN and CC) to isolate its individual effect on wasp abundance. We then developed models combining forest type with local predictors (dead wood volume, dead wood diversity, and local connectivity at 0.5 km). Due to moderate to strong correlations among these variables, each was included in a separate model. Similarly, we created models that combined forest type with regional predictors (mean temperature, mean precipitation, regional connectivity at 20 km). Finally, “full” models were constructed by combining forest type with both local and regional predictors, ensuring that no correlated predictor combinations were included in the same model. When evaluating local and regional predictors, we included forest type as a control covariate to account for broad management differences. However, forest type coefficients from these models were not interpreted because dead wood and connectivity differ between forest types (i.e. within site pairs) in our study system (Asplund et al. 2024). To isolate management effects, forest type was evaluated in the forest type model, which included forest type and year as fixed effects.

Models were compared using Akaike's Information Criterion (AIC) (Akaike 1973), and models with lower AIC values were considered better supported (Burnham and Anderson 2002; Johnson and Omland 2004). AIC comparisons were performed separately for each response variable.

Additional model checks included assessing multicollinearity using variance inflation factors (VIF), testing for singularity, and calculating R-squared values to evaluate explanatory power using the performance package version 0.13.0 (Lüdecke et al. 2021). Models with low collinearity (VIF < 5) (James et al. 2021) were retained. Models without diagnostic issues were kept for subsequent interpretation. Singular fits were accepted when the random-effect variance approached zero, indicating low among-site variability rather than a model-fitting issue. In such cases, the singular model still had the lowest AIC and was therefore retained.

We extracted model estimates using the sjPlot package version 2.8.15 (Lüdecke 2023), specifically the $tab_{\mathrm{mod}}\,el()$ function, which outputs fixed effect estimates as incidence rate ratios (IRRs). IRRs represent the multiplicative change in expected count associated with a one-unit increase in a given predictor (Hilbe 2011). For the categorical predictor "forest type," IRRs indicate the expected change in abundance in NN compared to CC.

We annotated p-values < 0.05 as significant but provided additional context for near-significant results.

## Results

In total, 1891 parasitoid wasps from the superfamily Ichneumonoidea were identified. Individuals were found in both forest management types (near-natural forest, NN, and formerly clear-cut forest, CC). Of the total, 1499 belonged to the family Ichneumonidae (824 in NN and 675 in CC), and 392 to the family Braconidae (197 in NN and 195 in CC). A total of 35 subfamilies were recorded (31 in NN and 31 in CC), with Phygadeuontinae being the most abundant (323 individuals; 176 in NN and 147 in CC) followed by Cryptinae (295 individuals; 218 in NN and 77 in CC) (Fig. 3).

As many as 810 individuals from nine subfamilies (8 in NN and 7 in CC) were grouped as generalists, whereas 1054 individuals from 23 subfamilies (20 in NN and 22 in CC) were grouped as specialists. Saproxylic Ichneumonoidea were associated with 11 subfamilies (10 in NN and 10 in CC), with a total of 661 individuals. The abundance of generalist-, specialist-, and saproxylic Ichneumonoidea can be seen in Appendix S1 of Online Resource 1.

Of the two ichneumonoid families and eight subfamilies assessed, Ichneumonidae had a 22% higher abundance in NN than in CC (IRR = 1.22, $p < 0.001$), and Ichneumoninae showed a 139% higher abundance in NN (IRR = 2.39, $p < 0.001$) (Table 1a). In contrast, Tryphoninae exhibited an opposite pattern, with a 76% lower abundance in NN relative to CC (IRR = 0.24, $p < 0.001$). Forest management did not significantly affect Braconidae or the other subfamilies in the forest type model.

## Effect of forest management on functional groups

Generalist Ichneumonoidea had a 64% higher abundance in NN than in CC (IRR = 1.64, $p < 0.001$), whereas specialists showed weak evidence for a 10% lower abundance in NN (IRR = 0.90, $p = 0.074$) (Table 1b). Saproxylic Ichneumonoidea were 36% more abundant in NN than in CC (IRR = 1.36, $p < 0.001$).

## The importance of local and regional habitat variables

Dead wood diversity was positively associated with the abundance of Braconidae, Phygadeuontinae, Orthocentrinae, Ichneumoninae, Alysiinae, and generalist and specialist Ichneumonoidea (Table 2a, Table 2b), indicating higher expected abundance with increasing dead wood diversity. In contrast, dead wood volume did not significantly affect any parasitoid group.

The importance of connectivity was taxon- and scale-dependent: Tryphoninae decreased with increasing local connectivity (0.5 km), whereas Cryptinae and saproxylic Ichneumonoidea increased with regional connectivity (20 km) (Table 2a, Table 2b). Furthermore, increased temperature was associated with lower abundance of several groups: Phygadeuontinae, Orthocentrinae, Euphorinae, and generalists, while Braconidae showed weak evidence of a similar negative trend ($p = 0.053$). In contrast, precipitation did not significantly affect any parasitoid group.

Table 1

**a** Forest type models across taxonomic groups. Results from generalized linear mixed models (GLMMs) showing incidence rate ratios (IRRs) for the effects of forest type (near-natural = NN; formerly clear-cut = CC) on Ichneumonoidea abundance. IRRs > 1 indicate higher abundance in NN relative to CC, whereas IRRs < 1 indicate lower abundance. p-values < 0.05 are shown in bold. N = number of site pairs; Observations = number of model observations; $R^2$ = marginal (fixed effects) / conditional (fixed + random effects) variance explained.

| Predictors | Ichneumonidae | | | Braconidae | | | Phygadeuontinae | | | Cryptinae | | | Orthocentrinae | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IRR | SE | p | IRR | SE | p | IRR | SE | p | IRR | SE | p | IRR | SE | p |
| Intercept | 38.91 | 9.31 | **< 0.001** | 14.38 | 2.35 | **< 0.001** | 9.25 | 2.21 | **< 0.001** | 3.66 | 2.13 | **0.026** | 7.85 | 1.89 | **< 0.001** |
| Forest type (NN) | 1.22 | 0.06 | **< 0.001** | 1.01 | 0.10 | 0.920 | 1.20 | 0.13 | 0.107 | 2.32 | 1.30 | 0.131 | 0.88 | 0.12 | 0.348 |
| Year (2023) | 1.86 | 1.07 | 0.284 | 1.16 | 0.43 | 0.698 | 1.47 | 0.82 | 0.485 | 1.67 | 1.93 | 0.660 | 0.98 | 0.55 | 0.978 |
| N | 12 | | | 12 | | | 12 | | | 12 | | | 12 | | |
| Observations | 24 | | | 24 | | | 24 | | | 24 | | | 24 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.105 / 0.976 | | | 0.012 / 0.776 | | | 0.053 / 0.878 | | | 0.098 / 0.672 | | | 0.008 / 0.815 | | |

Table 1
a continued

| Predictors | Euphorinae | | | Ichneumoninae | | | Tryphoninae | | | Campopleginae | | | Alysiinae | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IRR | SE | p | IRR | SE | p | IRR | SE | p | IRR | SE | p | IRR | SE | p |
| Intercept | 5.82 | 1.40 | **< 0.001** | 2.14 | 0.81 | **0.042** | 0.60 | 0.42 | 0.467 | 4.24 | 1.25 | **< 0.001** | 4.36 | 1.14 | **< 0.001** |
| Forest type (NN) | 0.80 | 0.13 | 0.180 | 2.39 | 0.44 | **< 0.001** | 0.24 | 0.05 | **< 0.001** | 1.05 | 0.41 | 0.897 | 0.91 | 0.31 | 0.781 |
| Year (2023) | 0.66 | 0.38 | 0.470 | 0.54 | 0.47 | 0.480 | 17.04 | 23.81 | **0.042** | 2.20 | 1.09 | 0.110 | 1.96 | 0.85 | 0.124 |
| N | 12 | | | 12 | | | 12 | | | 12 | | | 12 | | |
| Observations | 24 | | | 24 | | | 24 | | | 24 | | | 24 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.065 / 0.745 | | | 0.177 / 0.886 | | | 0.364 / 0.957 | | | NA | | | NA | | |

Table 1

**b** Forest type models across functional groups. Results from generalized linear mixed models (GLMMs) showing incidence rate ratios (IRRs) for the effects of forest type (near-natural = NN; formerly clear-cut = CC) on Ichneumonoidea abundance. IRRs > 1 indicate higher abundance in NN relative to CC, whereas IRRs < 1 indicate lower abundance. p-values < 0.05 are shown in bold. N = number of site pairs; Observations = number of model observations; $R^2$ = marginal (fixed effects) / conditional (fixed + random effects) variance explained.

| Predictors | Generalist | | | Specialist | | | Saproxylic | | |
|---|---|---|---|---|---|---|---|---|---|
| | IRR | SE | p | IRR | SE | p | IRR | SE | p |
| Intercept | 17.03 | 4.76 | **< 0.001** | 35.69 | 5.90 | **< 0.001** | 17.52 | 4.09 | **< 0.001** |
| Forest type (NN) | 1.64 | 0.12 | **< 0.001** | 0.90 | 0.06 | 0.074 | 1.36 | 0.11 | **< 0.001** |
| Year (2023) | 1.41 | 0.95 | 0.605 | 2.00 | 0.78 | 0.078 | 1.34 | 0.74 | 0.601 |
| N | 12 | | | 12 | | | 12 | | |
| Observations | 24 | | | 24 | | | 24 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.097 / 0.966 | | | 0.211 / 0.935 | | | 0.065 / 0.938 | | |

Table 2

**a** Best-supported AIC models across taxonomic groups. Results from generalized linear mixed models (GLMMs) selected using AIC, showing incidence rate ratios (IRRs) for the effects of local and regional environmental predictors on Ichneumonoidea abundance. Continuous predictors were standardized (std; z-score transformation), such that IRRs represent the multiplicative change in expected abundance associated with a one-standard-deviation increase in the predictor. Forest type was included as a control covariate but was not interpreted because dead wood and connectivity differ between forest types in the study system. p-values < 0.05 are shown in bold. N = number of site pairs; Observations = number of model observations; $R^2$ = marginal (fixed effects) / conditional (fixed + random effects) variance explained.

| **Predictors** | **Ichneumonidae** | | | **Braconidae** | | | **Phygadeuontinae** | | | **Cryptinae** | | | **Orthocentrinae** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **IRR** | **SE** | **p** | **IRR** | **SE** | **p** | **IRR** | **SE** | **p** | **IRR** | **SE** | **p** | **IRR** | **SE** | **p** |
| Intercept | 53.31 | 15.48 | **< 0.001** | 18.33 | 3.64 | **< 0.001** | 15.41 | 3.01 | **< 0.001** | 3.19 | 1.55 | **0.017** | 11.97 | 2.60 | **< 0.001** |
| Forest type (NN) | 0.69 | 0.32 | 0.431 | 0.59 | 0.18 | 0.087 | 0.37 | 0.13 | **0.004** | 2.95 | 1.78 | 0.072 | 0.27 | 0.08 | **< 0.001** |
| Dead wood volume (std) | | | | | | | | | | | | | | | |
| Dead wood diversity (std) | 1.53 | 0.40 | 0.101 | 1.43 | 0.22 | **0.019** | 1.89 | 0.31 | **< 0.001** | | | | 1.88 | 0.27 | **< 0.001** |
| Connectivity (0.5km std) | | | | | | | | | | | | | | | |
| Connectivity (20km std) | 1.29 | 0.24 | 0.169 | | | | | | | 2.70 | 0.84 | **0.001** | | | |
| Mean temperature (std) | | | | 0.78 | 0.10 | 0.053 | 0.59 | 0.08 | **< 0.001** | | | | 0.63 | 0.12 | **0.013** |
| Mean precipitation (std) | 1.25 | 0.23 | 0.227 | | | | | | | | | | | | |
| Year (2023) | 3.44 | 1.71 | **0.013** | 1.71 | 0.58 | 0.111 | 2.96 | 1.03 | **0.002** | 8.57 | 7.97 | **0.021** | 1.96 | 0.95 | 0.166 |
| N | 12 | | | 12 | | | 12 | | | 12 | | | 12 | | |
| Observations | 24 | | | 24 | | | 24 | | | 24 | | | 24 | | |
| Marginal $R^2$ / Conditional $R^2$ | NA | | | 0.323 / 0.353 | | | NA | | | NA | | | 0.546 / 0.849 | | |

Table 2
a continued

| Predictors | Euphorinae | | | Ichneumoninae | | | Tryphoninae | | | Campopleginae | | | Alysiinae | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | IRR | SE | p | IRR | SE | p | IRR | SE | p | IRR | SE | p | IRR | SE | p |
| Intercept | 4.72 | 1.19 | **< 0.001** | 3.47 | 1.20 | **< 0.001** | 0.13 | 0.13 | **0.036** | 3.78 | 0.78 | **< 0.001** | 6.34 | 1.53 | **< 0.001** |
| Forest type (NN) | 0.94 | 0.22 | 0.795 | 0.86 | 0.42 | 0.751 | 1.74 | 0.84 | 0.251 | | | | 0.28 | 0.12 | **0.004** |
| Dead wood volume (std) | 0.71 | 0.16 | 0.135 | | | | | | | | | | | | |
| Dead wood diversity (std) | | | | 1.71 | 0.43 | **0.034** | | | | | | | 1.97 | 0.39 | **0.001** |
| Connectivity (0.5km std) | | | | | | | 0.15 | 0.07 | **< 0.001** | | | | | | |
| Connectivity (20km std) | | | | 1.43 | 0.36 | 0.156 | | | | | | | | | |
| Mean temperature (std) | 0.62 | 0.15 | **0.042** | | | | | | | | | | 0.77 | 0.13 | 0.127 |
| Mean precipitation (std) | | | | 1.54 | 0.43 | 0.128 | 3.24 | 2.76 | 0.167 | | | | | | |
| Year (2023) | 1.10 | 0.67 | 0.878 | 0.98 | 0.66 | 0.979 | 42.17 | 74.02 | **0.033** | 2.44 | 1.09 | **0.046** | 3.30 | 1.32 | **0.003** |
| N | 12 | | | 12 | | | 12 | | | 12 | | | 12 | | |
| Observations | 24 | | | 24 | | | 24 | | | 24 | | | 24 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.373 / 0.805 | | | 0.538 / 0.821 | | | 0.637 / 0.974 | | | 0.210 / 0.686 | | | NA | | |

Table 2
**b** Best-supported AIC models across functional groups. Results from generalized linear mixed models (GLMMs) selected using AIC, showing incidence rate ratios (IRRs) for the effects of local and regional environmental predictors on Ichneumonoidea abundance. Continuous predictors were standardized (std; z-score transformation), such that IRRs represent the multiplicative change in expected abundance associated with a one-standard-deviation increase in the predictor. Forest type was included as a control covariate but was not interpreted because dead wood and connectivity differ between forest types in the study system. p-values < 0.05 are shown in bold. N = number of site pairs; Observations = number of model observations; $R^2$ = marginal (fixed effects) / conditional (fixed + random effects) variance explained.

| Predictors | Generalist | | | Specialist | | | Saproxylic | | |
|---|---|---|---|---|---|---|---|---|---|
| | IRR | SE | p | IRR | SE | p | IRR | SE | p |
| Intercept | 29.38 | 8.33 | **< 0.001** | 47.42 | 7.52 | **< 0.001** | 18.79 | 4.46 | **< 0.001** |
| Forest type (NN) | 0.50 | 0.21 | 0.095 | 0.48 | 0.06 | **< 0.001** | 1.39 | 0.46 | 0.325 |
| Dead wood volume (std) | | | | | | | | | |
| Dead wood diversity (std) | 1.86 | 0.43 | **0.007** | 1.50 | 0.10 | **< 0.001** | | | |
| Connectivity (0.5km std) | | | | | | | | | |
| Connectivity (20km std) | | | | | | | 1.58 | 0.26 | **0.006** |
| Mean temperature (std) | 0.56 | 0.11 | **0.002** | | | | | | |
| Mean precipitation (std) | | | | | | | | | |
| Year (2023) | 3.39 | 1.82 | **0.023** | 2.12 | 0.76 | **0.036** | 1.79 | 0.94 | 0.265 |
| N | 12 | | | 12 | | | 12 | | |
| Observations | 24 | | | 24 | | | 24 | | |
| Marginal $R^2$ / Conditional $R^2$ | 0.523 / 0.654 | | | 0.407 / 0.942 | | | 0.394 / 0.441 | | |

## Discussion

The purpose of this study was to assess the long-term effects of forest management on the abundance within Ichneumonoidea families and subfamilies in spruce-dominated forests in southeastern Norway. Overall, parasitoid wasp abundance showed taxon-specific responses to forest management. Ichneumonidae and Ichneumoninae were more abundant in near-natural forests, whereas Tryphoninae was more abundant in formerly clear-cut forests. Generalist and saproxylic Ichneumonoidea were more abundant in near-natural forests, whereas specialists showed only weak responses. In addition, variation in abundance was influenced by environmental factors, particularly dead wood diversity and spatial connectivity, with effects that were taxon- and scale-dependent.

# Taxon-specific responses to forest management

Ichneumonoid families and subfamilies responded differently to forest management history. Ichneumonidae, and especially Ichneumoninae, were more abundant in near-natural forests, whereas Tryphoninae showed higher abundance in formerly clear-cut forests.

Previous findings have shown that parasitoid abundance increases with greater stand structural complexity, a relationship mediated by the availability of suitable hosts (Rappa et al. 2024). In our study system, near-natural forests contain substantially higher levels of structural complexity than formerly clear-cut forests (Asplund et al. 2024). Consequently, near-natural forests are likely to offer more suitable hosts and microhabitats for Ichneumonidae and Ichneumoninae, which may help explain their higher abundance in these forests.

Long-term surveys in Belgium have documented substantial declines of Ichneumoninae species in disturbed landscapes (Thirion 1976, 1981, cited in Mayhew et al. 2009; Shaw and Hochberg 2001), likely reflecting reductions in their lepidopteran hosts (Mayhew et al. 2009; Shaw and Hochberg 2001). As we did not identify the parasitoid wasps to species level, we cannot accurately assess their exact host associations. At the same time, saproxylic beetles, a known host group for Ichneumonidae (Hilszczański 2018), did not differ in overall species richness or abundance between the two forest types (Norkute et al. 2025). This suggests that other host groups or factors such as microhabitat availability may better explain the observed variation in parasitoid abundance.

Several Ichneumoninae hibernate as adults and may require specific sites to do so, such as living or dead trees, grass tussocks, under stones or moss, or within dense conifer foliage near the soil surface (Verheyde et al. 2025; Verheyde and Quicke 2022). These structural conditions are potentially easier to locate in forests with greater volume of dead wood and vascular plant cover, as is the case for the near-natural forest stands in our study system (Asplund et al. 2024; Asplund et al. 2026). Furthermore, sources of sugar, such as nectar and honeydew, are important for the survival of many adult parasitoids (Jervis et al. 1993; Quicke 2015; Shaw 2006). The higher vascular plant cover and potentially more heterogeneous light conditions in near-natural forests (Asplund et al. 2024; Asplund et al. 2026) could provide greater access to nectar or habitats for honeydew-producing insects.

In contrast to Ichneumoninae, Tryphoninae showed higher abundance in formerly clear-cut forests. However, as many as 76% (105 individuals) of all identified Tryphoninae were found at a single formerly clear-cut site (Marker). Further examination showed that all specimens were identified as *Exenterus abruptorius*, a species known to parasitize diprionid sawflies such as *Neodiprion sertifer* (Broad et al. 2018). A local concentration of *Neodiprion sertifer* could therefore explain the unusually high numbers of *Exenterus abruptorius* recorded at this site. Although the statistical model did not classify this site as an outlier, caution is warranted when interpreting the broader forest-type pattern given the strong influence of a single site.

# Functional-group responses to forest management

Generalist Ichneumonoidea (idiobionts) were more abundant in near-natural forests, whereas specialist Ichneumonoidea (koinobionts) showed a tendency towards higher abundance in the formerly clear-cut forests. This result contrasts with patterns reported in earlier studies (Hilszczański et al. 2005; Stenbacka et al. 2010), which found higher abundances of idiobionts in recent clear-cuts and higher abundances of koinobionts in mature managed and old-growth forests. A key difference between the studies of Hilszczański et al. (2005) and Stenbacka et al. (2010) and ours lies in the temporal scale and forest categories being compared. In our study, formerly clear-cut stands had a mean stand age of 67 ± 3.3 years, whereas near-natural stands were substantially older (137 ± 6.8 years) (Asplund et al. 2024). In contrast, the clear-cuts examined by Hilszczański et al. (2005) and Stenbacka et al. (2010) were created around 2000–2001 and therefore represent much earlier successional stages (i.e. within the first decade after clear-cutting). Their “mature managed” forest stands (mean stand age of 108 years) are likely more comparable to our near-natural forests, as both have been subjected to selective logging rather than modern clear-cut management. The difference in stand history suggests that generalists may benefit from the open, early-successional conditions of recent clear-cuts, but not necessarily from the denser, later-successional structure of long-regenerated clear-cut forests. In addition, Hilszczański et al. (2005) and Stenbacka et al. (2010) focused specifically on saproxylic Ichneumonoidea, which limits direct comparability with our functional-group approach that includes both saproxylic and non-saproxylic taxa.

We defined our generalists by their idiobiont lifestyle, which requires sustained access to adult food resources, such as nectar, honeydew, or host-derived nutrients, to continue egg maturation throughout their lifespan (Hilszczański 2018; Quicke 2015). Near-natural forests in our study system exhibited substantially higher vascular plant cover and greater structural heterogeneity than formerly clear-cut forests (Asplund et al. 2024; Asplund et al. 2026), which may provide a wider array of feeding sites and host microhabitats for generalists. In contrast, specialists defined by a koinobiont

lifestyle typically emerge with developed eggs. Although they may consume nutrients as adults, they are unlikely to be as dependent on sustained adult feeding for egg maturation as the generalists (Hilszczański 2018; Quicke 2015). Consequently, the abundance of specialists may be more strongly influenced by the availability and distribution of suitable host taxa than by differences in adult resource availability. If their host communities are broadly similar between near-natural and formerly clear-cut forests, strong differences in their abundance may therefore not be expected. However, slightly higher densities of some host taxa in formerly clear-cut forests could contribute to the observed pattern. In addition, variation among specialist subfamilies may have weakened their overall response to forest management.

The interpretation of generalist and specialist responses to forest management is complicated by uncertainty in life-history information. Idiobiont and koinobiont are idealized strategies (Askew and Shaw 1986; Quicke 2015), and the common assumption that idiobionts are generalists and koinobionts specialists is not universally valid (Althoff 2003; Broad et al. 2018; Quicke 2015). Host ranges are often poorly resolved at the species level, and host records can be incomplete or unreliable (Hilszczański 2018; Quicke 2015; Shaw 2017; Shaw 2023). Even congeners can differ markedly in host breadth, both among koinobionts and idiobionts (Shaw 2006). This variability highlights how functional-group assignments simplify diverse biological strategies. Taking our most abundant subfamily, Phygadeuontinae, as an example, although most known species are considered idiobionts, some genera (e.g. *Atractodes*, *Mesoleptus* and *Stilpnus*) may be koinobiont (Broad et al. 2018), meaning that our classification of the entire subfamily as idiobiont overlooks some underlying variation. Idiobionts can also show ecological specialization in certain taxa, e.g. *Scambus* and *Rhyssa persuasoria* (Broad et al. 2018; Fitton et al. 1988), while some koinobionts can exploit multiple hosts or switch hosts across generations (Althoff 2003; Broad et al. 2018; Hilszczański 2018; Quicke 2015; Shaw et al. 2016). Together, these factors suggest that specialization patterns should be interpreted cautiously and that species-level data would be needed to fully resolve how forest management affects parasitoid specialisation.

When grouping parasitoid wasps according to their association with dead wood, saproxylic Ichneumonoidea were more abundant in near-natural than in formerly clear-cut forests. This indicates that forest management history can have long-lasting effects on ichneumonoid parasitoids associated with saproxylic hosts. The greater structural heterogeneity in near-natural forests (Asplund et al. 2024) may provide suitable habitat and resources for saproxylic hosts, which in turn sustain the parasitoid wasps. This pattern is consistent with the responses reported for saproxylic koinobionts in mature forests that have not been recently clear-cut (Hilszczański et al. 2005; Stenbacka et al. 2010). In contrast, saproxylic idiobionts showed different responses in those studies than observed here. These differences likely reflect, in part, the shorter time since clear-cutting in those studies, but may also relate to differences in species composition and to the fact that we did not distinguish between saproxylic idiobionts and koinobionts, instead combining them into a single functional group. Functional-group responses should therefore be interpreted cautiously, as aggregation at the subfamily or functional-group level may obscure species-specific responses of saproxylic parasitoids to forest management.

## The importance of local and regional habitat variables

Dead wood diversity was positively associated with several taxa. This is consistent with earlier work showing that different types of dead wood, such as standing versus downed wood, support distinct parasitoid wasp assemblages (Hilszczański et al. 2005). Parasitoid wasp abundance has been reported to be higher on standing than on downed dead wood (i.e. snags versus logs), likely because hosts developing in snags are more physically accessible than those in logs in contact with the ground or surrounding vegetation (Ulyshen et al. 2011). Similarly, parasitoid abundance has been shown to increase with increasing standing dead wood, highlighting the importance of forest structural elements for supporting parasitoid populations (Rappa et al. 2024). Because the dead wood diversity metric integrates both the amount and heterogeneity of dead wood resources, including variation in tree species, decay stage, size, and the quantity of different dead wood types (Hottola et al. 2009; Norkute et al. 2025), the positive associations observed in our study likely reflect the importance of resource heterogeneity rather than resource quantity alone. Interestingly, saproxylic Ichneumonoidea did not respond to dead wood diversity despite being more abundant in near-natural forests, suggesting that near-natural forest conditions encompass additional long-term structural and ecological features influencing saproxylic taxa that are not fully captured by the variables we have measured.

In contrast, dead wood volume did not affect any parasitoid group, including saproxylic Ichneumonoidea. This suggests that the quantity of dead wood alone may be a poor predictor of parasitoid wasp abundance. Similarly, Gibb et al. (2008) found that parasitoid wasps associated with wood-boring beetles were not more abundant at sites with higher dead wood volume, indicating that local increases in dead wood volume do not necessarily translate into greater parasitoid abundance.

Beyond local structural features, the spatial configuration of old spruce forest patches may shape parasitoid communities. In our study, we measured connectivity at both local (0.5 km) and regional (20 km) scales, revealing taxon- and scale-dependent effects: Tryphoninae responded negatively to local connectivity, whereas Cryptinae and saproxylic Ichneumonoidea increased with regional connectivity. The negative response of Tryphoninae to local connectivity is consistent with their higher abundance in formerly clear-cut forests. However, the pattern may have been influenced by the high concentration of Tryphoninae individuals at a single formerly clear-cut site (Marker). For Cryptinae and saproxylic Ichneumonoidea, higher regional connectivity may increase the probability of encountering suitable host populations across the landscape. Such contrasting responses are consistent with previous work showing that dispersal ability varies widely among parasitoid wasps, from poorly dispersing taxa to species capable of moving over relatively large distances in relation to their hosts (Couchoux et al. 2016; Cronin and Reeve 2005; Gibb et al. 2008; Jonsell et al. 1999; Komonen et al. 2000).

In addition to habitat amount and connectivity, environmental gradients such as temperature and precipitation may further shape parasitoid communities. Temperature showed a consistently negative association with several parasitoid groups, including Phygadeuontinae, Orthocentrinae, Euphorinae, and generalists, while Braconidae showed weak evidence of a similar trend. Such responses suggest that higher mean near-ground temperatures during the sampling season may constrain parasitoid activity or host availability. Temperature is a key cue influencing insect phenology, development, and host–parasitoid synchrony (Forrest 2016; Hance et al. 2007). For Ichneumonidae in particular, reliance on precise seasonal timing, combined with diverse overwintering and diapause strategies, may make some taxa more sensitive to temperature variation than others (Quicke 2015; Verheyde et al. 2025; Verheyde and Quicke 2022). However, whether the observed effects reflect direct physiological constraints or indirect effects mediated through hosts and their associated resources cannot be resolved here. In contrast to temperature, precipitation did not affect any parasitoid group. Precipitation is known to influence forest insects primarily through indirect pathways, such as tree growth and decay, which in turn create the habitat and food resources for herbivores, saproxylic species, and their parasitoids (Battisti and Larsson 2023; Hilszczański 2018; Stokland et al. 2012; Ulyshen and Šobotník 2018). However, in our study, mean precipitation over the sampling season may not capture the fine-scale moisture conditions experienced by parasitoids or their hosts. Consistent with this interpretation, broad-scale analyses have found weak or inconsistent relationships between rainfall and parasitoid assemblage size (Hawkins 1990).

Overall, the patterns observed in this study indicate that taxon-specific differences in parasitoid wasp abundance are shaped by interactions between local habitat structure, landscape configuration, and environmental conditions.

## Conclusion

Our study demonstrates that forest management history can have long-lasting, taxon-specific effects on parasitoid wasp abundance in boreal spruce forests. Near-natural forests generally supported higher parasitoid wasp abundances than formerly clear-cut forests, although responses varied among taxa and functional groups. Dead wood diversity, rather than dead wood volume, was positively associated with multiple parasitoid wasp groups, while habitat connectivity and temperature showed taxon-dependent effects, with connectivity responses varying between local and regional spatial scales.

These findings indicate that retaining near-natural forest conditions, promoting diverse dead wood structures, and maintaining regional connectivity of old spruce forests may help sustain parasitoid wasp populations and the ecological functions they provide in boreal forest ecosystems.

Interpreting abundance patterns remains challenging due to incomplete knowledge of parasitoid wasp life histories and host associations. Emerging molecular tools such as DNA metabarcoding offer opportunities to improve taxonomic resolution (Liu et al. 2020), but incomplete reference libraries for Hymenoptera (Åström et al. 2023) and the lack of reliable abundance estimates mean that morphological identification remains essential for validating molecular data and interpreting ecological patterns. Continued synthesis of taxonomic and ecological knowledge (Broad et al. 2018; Hilszczański 2018; Quicke 2015), together with species-level identification and information on host use, dispersal ability, and forest structural dynamics, will be key to improving our understanding of how forest management shapes parasitoid wasp abundance.

## Declarations

# Competing interests

The authors declare that they have no competing interests.

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# Author Contribution

B.M.H. conceived the study together with T.B. and L.F.L. B.M.H. conducted the fieldwork, performed the data analyses, and wrote the first draft of the manuscript. T.B. and L.F.L. contributed to the study design, interpretation of the results, and critical revision of the manuscript. L.F.L. provided substantial support with statistical analyses. All authors read and approved the final manuscript.

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# Data Availability

The dataset supporting the findings of this study has been deposited in DataverseNO and will be made publicly available upon publication of the article. The dataset can be made available to reviewers during the review process upon reasonable request.

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## Figures



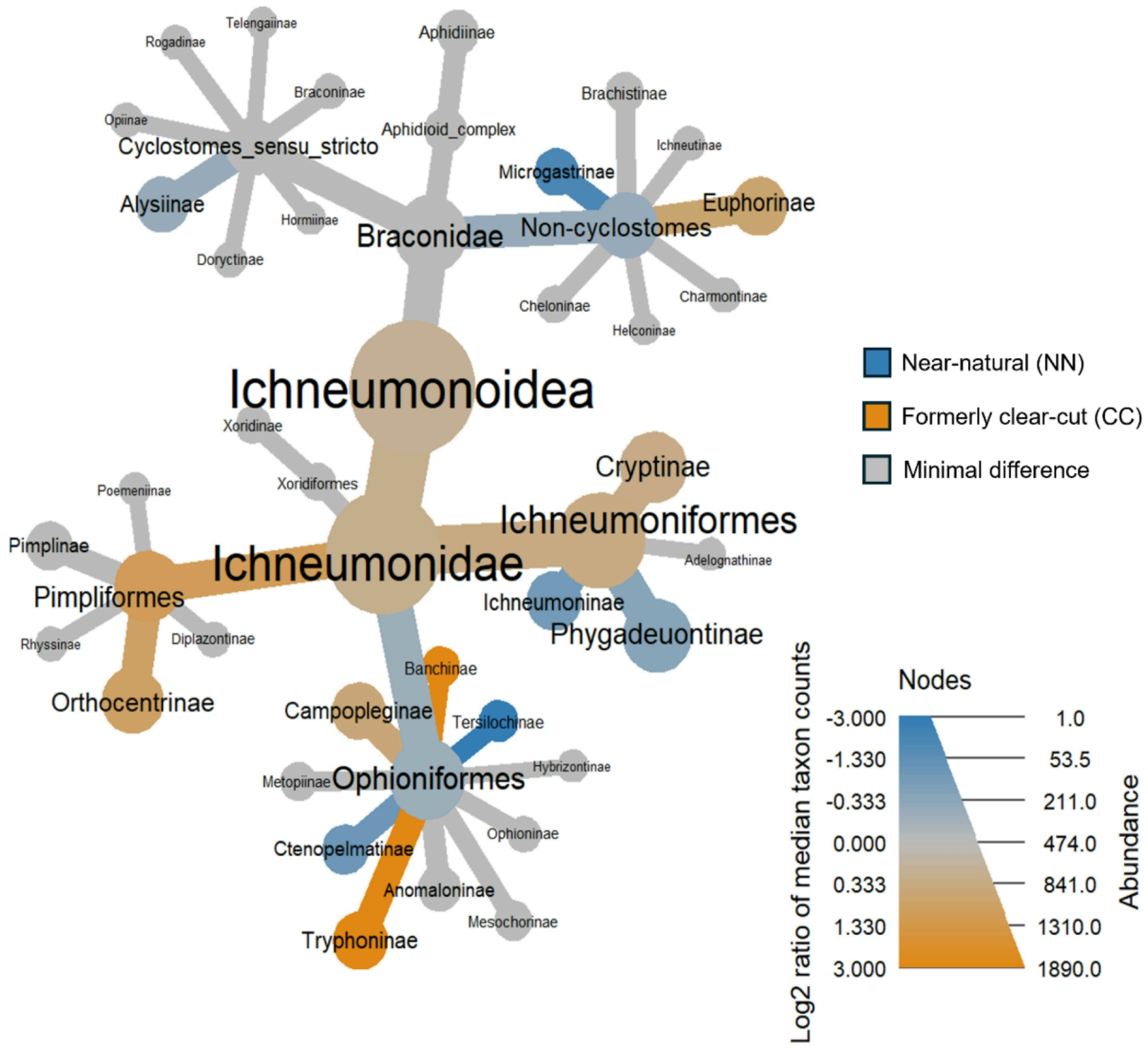

**Figure 1**

Location of the twelve site pairs in southeastern Norway. Reproduced from Asplund et al. (2024), licensed under CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/)



**Figure 2**

Malaise trap placement at the NN site in location 11 (Marker). Photo: Brian Moe Holter




**Effect of forest management within families and subfamilies**

**Figure 3**

Taxonomic heat tree illustrating the distribution and total abundance of Ichneumonoidea taxa between two forest management types: near-natural (NN) and formerly clear-cut forests (CC). Node size reflects the total number of individuals (taxon abundance) across all plots, while node colour represents the $\log_2$ ratio of median taxon counts between the forest types. Blue nodes indicate higher median counts in NN, orange nodes indicate higher median counts in CC, and grey nodes reflect minimal differences. The colour scale ranges from −3 to +3. Total taxon abundance did not differ significantly between the forest types according to the built-in test in the R package metacoder (Wilcoxon rank-sum test, $p > 0.1$; however, see Table 1a for GLMM-based effects within taxa)

## Supplementary Files

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