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Long-term effects of forest management on parasitoid wasps

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Master of Science in Ecology

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Abstract

Forest ecosystems are important for maintaining multiple ecosystem services, providing timber and habitat for pest controlling species. Parasitoid wasps are important natural pest controls, but studies on how parasitoid wasps are influenced by forestry are scarce. Clear-cutting is an intensive forest management practice used in Norway, and the forests that were clear-cut in the 1940s-1960s have recently reached a state that can be compared with mature forests that have been exposed to selective cutting in the past (termed near-natural). Studying the abundance of parasitoid wasps between the two forest management types, could yield valuable insights into the most effective forest management practices for maintaining a robust population of these beneficial insects over the long-term.

To compare the two forest management types on parasitoid wasps, I collected and sorted specimens of parasitoid wasps (Hymenoptera, Ichneumonoidea) from 12 locations. Each location had two field areas – one in a former clear-cut forest and one in a near-natural forest – in southeastern Norway. The collection was done using Malaise traps.

I found that the abundance of parasitoid wasps was similar in mature clear-cut forests and near-natural forests at the family level. However, at the subfamily level, there were greater variation with some subfamilies being more abundant in near-natural forests.
Interestingly, one family, one subfamily and generalist species showed increased abundance with the increase of total volume of dead wood, but this pattern did not hold true for saproxylic Ichneumonoidea.

Investigating the impacts of forest management at the family level may be overly broad due to the presence of numerous subfamilies with different life history strategies. To enhance clarity, it is essential to study these parasitoid wasps at the lowest possible taxonomic level.
The complexity in the observed variation in parasitoid wasp abundance between the forest management types makes it difficult to conclude which forest management practice yields the most abundant parasitoid community.

Table of contents

1. Introduction

The demand for wood as a timber and fuel source throughout history, combined with the technological advancements in forestry has led to deforestation and intensive forest management, which in turn have given rise to long-lasting detrimental effects on biodiversity, forest ecosystems and their ecosystem services (Esseen et al., 1997; IPBES et al., 2019; Kuuluvainen et al., 2012; Lundmark et al., 2013; McEwan et al., 2020; Perlin, 2005; Pohjanmies et al., 2017; Rodriguez et al., 2019; Siitonen, 2001; Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010; Ulyshen & Šobotník, 2018; Watson et al., 2018). When forests are managed intensively only for specific goods like timber, many of the ecosystem services may be overlooked and consequently undervalued (Thompson et al., 2011). This has been the case for natural pest control which is one of the ecosystem services that are least understood when it comes to the impact of forestry (Pohjanmies et al., 2017).

Natural pest control (natural biological control in Stenberg et al. (2021a, 2021b)) can be defined as the regulation of a pest population by predators, herbivores, parasitoids, or pathogens without intentional human intervention (Stenberg et al., 2021a, 2021b). The pest population is thereby naturally kept below what is considered a damage threshold for humans (Stenberg et al., 2021a, 2021b). An important natural pest control is parasitoid wasps, wasps (Hymenoptera) whose larvae feed on, and subsequently kill, their arthropod host (Godfray, 1994; Gullan & Cranston, 2014; Hilszczański, 2018; Hilszczański et al., 2005). They are one of the most ecologically diverse and numerous groups of insects (Forbes et al., 2018; Gaston, 1991; Hilszczański, 2018; Hilszczański et al., 2005). In forests, parasitoid wasps may reduce the populations of bark beetles and different wood boring insects that may damage trees (Hilszczański, 2018; Kenis & Hilszczanski, 2004; Quicke, 2015). However, studies on how parasitoid wasps are influenced by forestry are scarce (but see Hilszczański et al. (2005) and Stenbacka, Hjältén, Hilszczański, Ball, et al. (2010)).

In Norway, more than half of all described species, including 48% of the threatened species, live in forests (Artsdatabanken, 2021; Framstad et al., 2018). In the light of the recent trends in insect decline (Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021), it is important to examine the effects of forest management on parasitoid wasps.

Clear-cutting, where most or all of the trees are removed from a forest area at a time, is the main forest management practice used in Norway (Seedre et al., 2018; Storaunet & Rolstad, 2020). However, the forestry in Norway has had a long history of intensive management before the dominance of clear-cutting, shifting from selective cutting, removing single trees or trees with a certain dimension, to clear-cutting around the 1940s (Storaunet & Rolstad, 2020; Storaunet et al., 2005). In 2016, only 30% of the productive forest in Norway had not been clear-cut (Storaunet & Rolstad, 2020). At present, clear-cutting is also the most important harvesting method in Finland and Sweden, but the timing and conversion from selective cutting varies (Kuuluvainen et al., 2012; Lundmark et al., 2013).

Clear-cutting with short rotation cycles of cutting and regeneration, often with planting of the same tree species, leads to homogenous, young, and even-aged forest stands, with low amounts of dead wood (Kuuluvainen et al., 2012; Seedre et al., 2018; Siitonen, 2001; Siitonen et al., 2000; Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010; Stokland et al., 2012). Compared with old-growth or previously selective cut forests, dead wood of large dimensions are particularly scarce as trees are removed before reaching their maximum age (Asplund et al., 2024; Esseen et al., 1997; Siitonen, 2001; Siitonen et al., 2000; Sippola et al., 1998; Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010; Stokland et al., 2012; Storaunet et al., 2005). By altering the forest in these ways, clear-cutting may lead to fragmentation and decreased continuity and connectivity of suitable forest habitat for several organisms that depend on continuous canopy cover and old-growth conditions (Asplund et al., 2024; Esseen et al., 1997; Fahrig, 2003; Komonen et al., 2000; Kuuluvainen & Gauthier, 2018; Moor et al., 2021; Nordén et al., 2014; Nordén et al., 2013; Siitonen, 2001; Stokland et al., 2012)

Forests that have not been clear-cut but subjected to selective cutting in the past (hereafter termed near-natural), have over time developed characteristics of a true natural forest; a heterogenous forest structure with varied tree dimensions and multi-layered canopies, older mean tree age, and greater volume of dead wood. (Jacobsen et al., 2020; Siitonen, 2001; Siitonen et al., 2000; Storaunet & Rolstad, 2020; Storaunet et al., 2005).

The larger volume of dead wood in near-natural forests compared to clear-cut forests may promote a greater biodiversity (Graf et al., 2022; Stokland et al., 2012; Storaunet et al., 2005; Ulyshen & Šobotník, 2018). Many different taxa, like insects, fungi, birds, and mammals depend, directly or indirectly, upon dead or dying wood (Birkemoe et al., 2018; Ferro, 2018; Graf et al., 2022; Speight, 1989; Stokland et al., 2012; Storaunet et al., 2005; Ulyshen & Šobotník, 2018). These organisms are termed saproxylic (Birkemoe et al., 2018; Ferro, 2018; Graf et al., 2022; Speight, 1989; Stokland et al., 2012; Ulyshen & Šobotník, 2018). It is estimated that about 20-30% of all forest insects in well studied areas of northern Europe are saproxylic (Siitonen, 2001; Stokland et al., 2012; Ulyshen & Šobotník, 2018). Dead wood can be used as a hiding place or nesting site where organisms can get protection from drought, cold, irradiation, and fire (Birkemoe et al., 2018; Ferro, 2018; Hilszczański, 2018; Stokland et al., 2012; Ulyshen & Šobotník, 2018). Dead wood also provides food directly to wood feeders, and indirectly to fungivores, predators and parasitoids (Birkemoe et al., 2018; Ferro, 2018; Hilszczański, 2018; Stokland et al., 2012; Ulyshen & Šobotník, 2018).

The majority of saproxylic parasitoids are in the order Hymenoptera (Hilszczański, 2018). Many of these parasitoid wasps, like in the superfamily Ichneumonoidea, target insects that feed beneath the bark in the phloem layer (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015).

Functionally, parasitoid wasps can be divided into koinobiont and idiobiont parasitoids (Askew & Shaw, 1986; Broad et al., 2018; Fitton et al., 1988; Godfray, 1994; E. Haeselbarth, 1978; E. v. Haeselbarth, 1978; Hilszczański, 2018; Quicke, 2015).

Koinobiont parasitoids allow their hosts to continue to feed and grow after they have been parasitized, thus delaying the killing of their hosts (Askew & Shaw, 1986; Broad et al., 2018; Fitton et al., 1988; Godfray, 1994; Hilszczański, 2018; Quicke, 2015). They can in some cases manipulate their hosts growth physiology, resulting in a delay in host maturation and pupation (Godfray, 1994; Hilszczański, 2018). Due to the difficulty of living outside of a host that crawls inside a tree, saproxylic koinobionts are endoparasitoids, meaning that they develop inside their host (Broad et al., 2018; Hilszczański, 2018). This development has led them to adapt to their hosts immune responses, making them mostly host-specific (Broad et al., 2018; Godfray, 1994; Hilszczański, 2018; Quicke, 2015). There are however exceptions, and some may be specialized to a particular niche, parasitizing different host with similar biology (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015).

Idiobionts permanently paralyze or kill their hosts after parasitism, not allowing their host to continue to feed and grow (Askew & Shaw, 1986; Broad et al., 2018; Fitton et al., 1988; Godfray, 1994; Hilszczański, 2018; Quicke, 2015). The saproxylic idiobionts are mostly ectoparasitoids, developing outside the host, due to the lack of threat from the immovable host larva, which, if alive, may squash the parasitoid (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015). By living outside the host, they have no need for an adaption to the hosts immune response and is therefore more likely to be host generalists (Broad et al., 2018; Godfray, 1994; Hilszczański, 2018; Quicke, 2015).

Specialists are generally more prone to extinction than generalists due to their lower flexibility in diet, niche, or biotope (Clavel et al., 2011; Dennis et al., 2011; McKinney, 1997). Species of higher trophic levels in the food chain are also more extinction prone than lower trophic levels (McKinney, 1997; Purvis et al., 2000). Thus, it would be expected that parasitoid wasps struggle as they inhabit high positions in trophic food chains, and that specialists like saproxylic koinobionts in particular may be more sensitive to the quality and continuity of forests than their hosts (Hilszczański, 2018; Shaw & Hochberg, 2001). Information on parasitoids can thus give a better indication of the state of the forest and provide valuable information to conservationists (Hilszczański, 2018; Shaw & Hochberg, 2001).

In Finland, the most specialized species in higher trophic levels has been shown to be vulnerable to extinction when exposed to a forest landscape with a history of clear-cutting (Komonen et al., 2000). Hilszczański et al. (2005) found that forest management type and dead wood characteristics significantly affected saproxylic beetle associated parasitoid (Hymenoptera, Ichneumonoidea) assemblages in Sweden. The specialists (koinobionts) were less abundant in recent clear-cut forest compared to old growth forest and mature managed forest, while the opposite was true for the generalists (idiobionts) (Hilszczański et al., 2005). In line with Hilszczański et al. (2005), a separate Swedish study also observed a similar pattern: koinobionts were more common in old-growth reserves and mature managed forests, while idiobionts were more abundant on clear-cuts (Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010).

The status and ecology of parasitoid wasps in Norway is not well known, and this is evident for the superfamily Ichneumonoidea (Elven & Søli, 2021; Ødegaard et al., 2021). Since parasitoid wasps are likely to be important for forest as natural pest controls (Hilszczański, 2018; Kenis & Hilszczanski, 2004), and with certain species or groups potentially vulnerable to forestry (Hilszczański et al., 2005; Komonen et al., 2000; Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010), investigating the long-term effects of forest management on this diverse group is essential.

In this master project, I will compare near-natural forest, hereafter NN, with mature clear-cut forest, hereafter CC, to investigate the long-term effects of forest management on the abundance of Ichneumonoidea families and subfamilies in spruce-forests in southeastern Norway.

Objectives:

1. Test if there is a difference in abundance of Ichneumonoid families and subfamilies between NN and CC.

2. Determine if there are differences in specialist and generalist Ichneumonoidea (koinobiont and idiobiont subfamilies) between the two forest management types.

3. Test if there is a difference in abundance of saproxylic Ichneumonoidea between NN and CC.

4. Understand to what extent dead wood volume drives the differences in abundance of Ichneumonoidea.

Predictions:

Near-natural forests have more heterogenous forest structure and greater volume of dead wood, and I expect that:

1. The abundance of Ichneumonoid families and subfamilies are greater in NN sites compared to CC sites.

2. NN contain a greater abundance of specialists (koinobionts) compared to generalists (idiobionts) meaning that the effect of forest management is affecting specialists more than generalists.

3. The abundance of saproxylic Ichneumonoidea are greater in NN sites compared to CC sites.

4. Greater abundance of saproxylic Ichneumonoidea with greater volume of dead wood.

2. Materials and methods

2.1 Study area and design

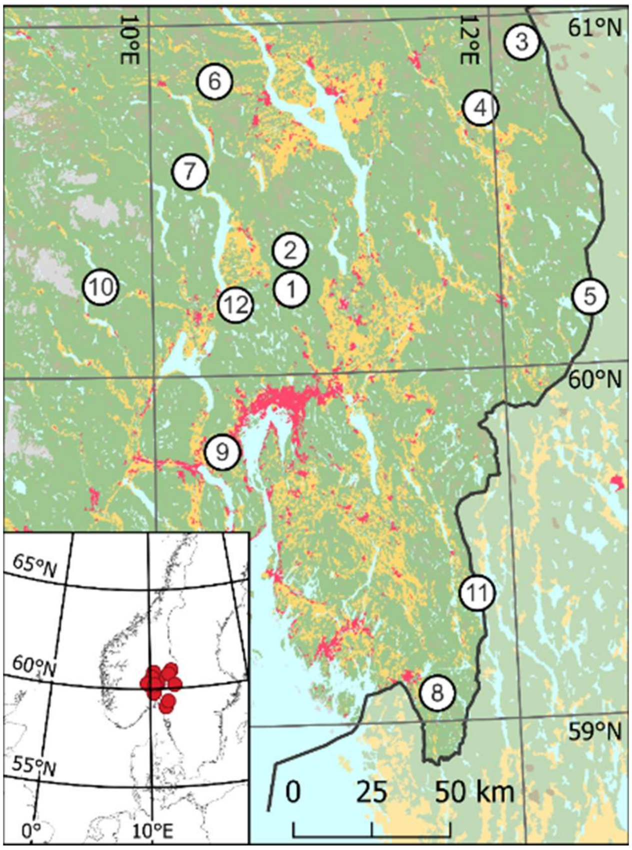

Figure 1. The locations of the EcoForest project. Source: Johan Asplund.

This study is a part of the EcoForest project, a competence and collaboration project financed by the Norwegian Research Council, focusing on the long-term effects of the clear-cutting forestry on biodiversity, carbon storage and functions in boreal forests of Norway.

The project examines how mature forests with a history of clear-cutting (CC) differs from forests without a history of clear-cutting (NN) (Ecoforest.no). The forests without a history of clear-cutting have been selective cut in the past, while the clear-cut forests were cut in the 1940's-1960's (Asplund et al., 2024).

Twelve locations in southeastern Norway are included (Figure 1, Appendix 1). Each location is divided into two sites (CC and NN), of mature boreal forest, dominated by Norway spruce (*Picea abies* (L.) H. Karst.). The distance between the sites is always less than 5 km (Asplund et al., 2024)

The site pairs have similar soil type, bedrock, slope, aspect, productivity, and elevation. The elevation between locations varied from 178 MASL (meters above sea level) to 668 MASL, with an average of 452 MASL across all the sites. None of the sites have any signs of fertilization, commercial thinning, drainage, or bark beetle (*Ips typographus*) attacks, while the near-natural sites are without any recent signs of human activity or dead wood removal (Asplund et al., 2024). See Asplund et al. (2024) for more detailed description of the site selection.

2.2 Insect trapping

Insects from location 1-10 were collected in 2022 by earlier students and staff joining the project. I collected insects in 2023 from location 11, Marker municipality, and location 12, Langvassbrenna in Jevnaker municipality (Figure 1, Appendix 1). For coordinates see Asplund et al. (2024).

Data collection was done with black and white Malaise traps (BugDorm, Taiwan) fastened to a living tree (Figure 2, Figure 3).

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 (Figure 3). In relation to a different project targeting insect DNA, the collection bottle was wrapped in aluminum foil in order to protect the DNA from UV-light and heat.

Figure 2. Malaise trap placement at the CC site in location 11 (Marker).
Photo: Brian Moe Holter

The traps were activated at the end of May and were emptied every two weeks, four times at each location, until the end of July/beginning of August. During collection, the bottles were labeled with the collection period, location, site, trap type, and cardinal direction. I used 96% ethanol the first 3 emptying periods and 85% ethanol the 4th, due to a mistake made in 2022. After each collection, the insects were placed in a -20 °C freezer at the Norwegian University of Life Sciences (NMBU).

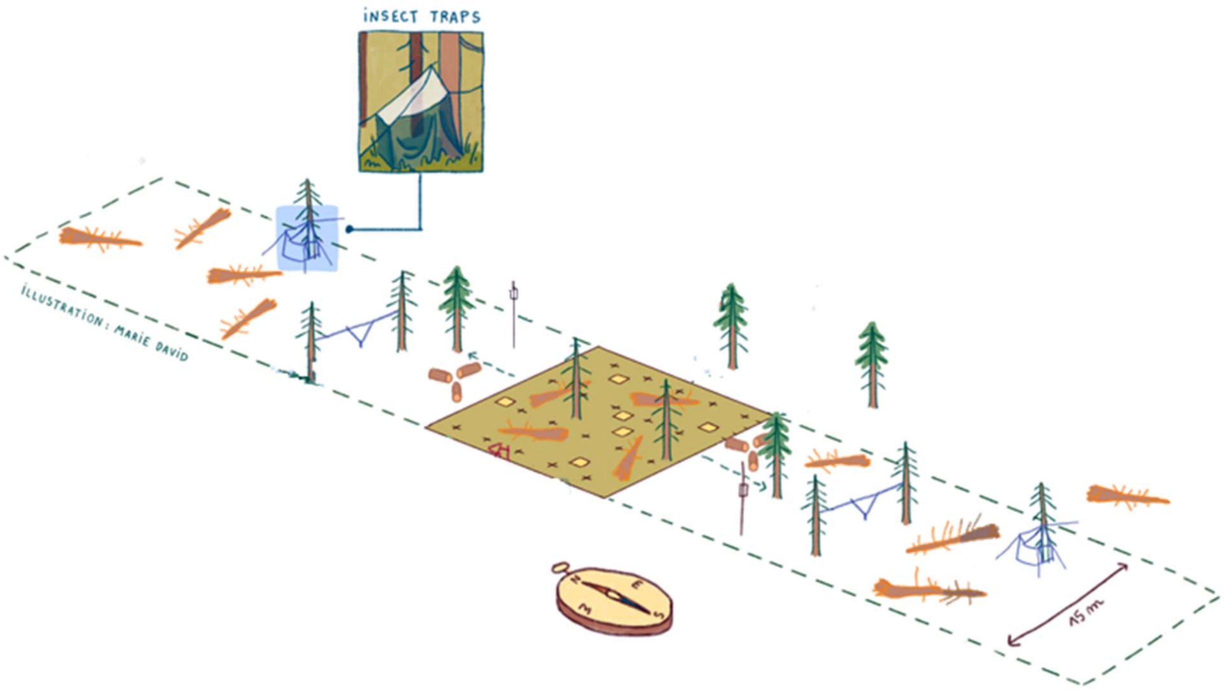

Figure 3. Sampling design highlighting the Malaise trap. Dead wood surveys were conducted in a north-south transect that measured 133.33 x 15 m (dashed outline) with a 15 x 15 m main plot at the center. The main plot had six sub-plots (yellow) where temperature (°C) was registered. Illustration by Marie David.

2.3 Insect sorting and identification

The insect samples were kept in the freezer until extraction of DNA through a lysation process. This process enabled DNA metabarcoding of the insects and was carried out by colleagues within the project. See Åström et al. (2023) for more details on this type of method. DNA metabarcoding has become a popular way of studying insects in recent years (Liu et al., 2020), but DNA reference libraries are not complete, especially for Hymenoptera (Åström et al., 2023). Thus, morphological identification of insects is important in order to verify the DNA-based studies in addition to get estimates of abundance which is still not available from metabarcoding. After lysation and DNA metabarcoding, the Malaise trap bottles were emptied through a fine sieve, separating the insects from the lysing solution (ATL buffer and proteinase K). The insects were subsequently placed in a petri dish with 85% ethanol. I used a stereo microscope to sort all insects into order and identify families and subfamilies of Hymenoptera. When samples included a large number of small Diptera (Sciaridae) (700-1000 individuals) I counted a subset, 1/4th of the petri dish, and multiplied by four to get the total number. My main focus was to identify the families and subfamilies within the superfamily Ichneumonoidea, which includes several saproxylic subfamilies (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015).

Tweezers, and pipettes for the smallest insects, were used to place each insect into glass vials filled with 85% ethanol. The vials were labelled with the information on collecting period, location, site, trap type, and cardinal direction.

Because of the extensive workload, I sorted insects from the traps to the north only, and from two periods of insect collection (1 and 3). Period 1 corresponds to the first half of June, and period 3 corresponds to the first half of July (Appendix 1). Some specimens of Ichneumonoidea were dried and subsequently pinned or card pointed. This made it easier to determine them to subfamily. I used the method for pinning and card pointing described in Broad et al. (2018).

Literature I used for identification of families of Ichneumonoidea, and subfamilies of Ichneumonidae was Broad et al. (2018). For identification of subfamilies of Braconidae I used: Goulet and Huber (1993), Nastasi et al. (2023), Karlsson (2005), and Hackston (2020) now updated to (Hackston, 2024) which include two additional sources, namely Shaw and Huddleston (1991) and Broad et al. (2016).

In addition to these sources, experts on Ichneumonoidea Alf Tore Mjøs and Jarl Birkeland assisted in the identification. In some cases, they identified down to genus and species level, and Alf Tore used two additional sources in the identification of two new species for Norway, namely Johansson (2020) and Johansson (2022).

Determining if the subfamilies were specialist, generalist or saproxylic was done by using the sources in Appendix 4. I annotated the subfamilies to “saproxylic” and “not saproxylic” based on Hilszczański (2018) with supplementary info on relevant wood living hosts from Broad et al. (2018) and Quicke (2015). I combined “saproxylic” and “partly saproxylic” due to a limited amount of “fully saproxylic” subfamilies in my samples. However, I found no information on the saproxylicity of the subfamily Brachistinae, which has gone through a lot of revisions recently. Brachistinae include several tribes formerly in Helconinae, as well as other tribes formerly in other subfamilies (Chen & van Achterberg, 2019; Sharanowski et al., 2011). Since Helconinae is placed as saproxylic in Hilszczański (2018), I chose to annotate Brachistinae as saproxylic as well.

It is important to note that the research on the phylogeny is recent with multiple sources giving different views (Chen & van Achterberg, 2019; Jasso-Martínez et al., 2022; Quicke, 2015; Sharanowski et al., 2011).

2.4 Environmental variables

All sites had a 15 x 15m main plot (Asplund et al., 2024) (Figure 3)

The different dead wood types and volumes (m^3ha^{-1}) were surveyed in a north-south transect that measured 133.33 x 15 m with the 15 x 15 m plot at the center (Asplund et al., 2024) (Figure 3). All dead wood that originated inside the transect with a diameter of ≥ 5 cm at breast height or at the base were measured (Asplund et al., 2024).

Each main plot had six sub-plots where temperature (°C) was registered (Figure 3). TMS-4 dataloggers (TOMST s.r.o.; Wild et al., 2019) registered temperature every 15 minutes at the center of each sub-plot, 15 cm above the ground (Asplund et al., 2024). Mean temperature was calculated for each site and period (Asplund et al., 2024).

Precipitation (mm/day) was calculated using data from the archives of Norwegian Meteorological Institute (MET Norway) THREDDS server. I downloaded seNorge2018_2022.nc and seNorge2018_2023.nc to get the data from 2022 and 2023. See Lussana et al. (2018); Lussana et al. (2019) for more details and background information on seNorge precipitation measurements, and see (MET Norway) for URL. Mean daily precipitation was calculated for each site and period.

Connectivity of old spruce forests, meaning how connected the sites are to old forest habitat, was calculated as the sum of living spruce volume (m^3ha^{-1}) from forests above 80 years old, within 25 km radius from the main plot and assuming a mean dispersal distance of 0.5 km. For more details on the connectivity measurements, see Asplund et al. (2024).

2.5 Data analysis

I created all my figures and performed statistical analyses using the software environment R version 4.3.3 (R Core Team, 2024) and RStudio version 2023.12.1+402 (Posit team, 2024).

I explored my data based on Zuur et al. (2010). My data is count data and right skewed. To avoid pseudoreplication, I accounted for the variation between the different sites by setting site as a random effect (Bolker et al., 2009; Harrison et al., 2018). Consequently, I analyzed my data with generalized linear mixed models (GLMMs) that combine linear mixed models (includes random effects) with generalized linear models that can be applied to non-normal data (Bolker et al., 2009). I intended to use Poisson distribution, which is often used with count data, but due to high overdispersion (more variance in the data than expected by the statistical model), I ended up choosing Negative binomial distribution with a log link (Bolker et al., 2009; Harrison, 2014; Harrison et al., 2018; Hilbe, 2011). The R package lme4 version 1.1-35.1 (Bates et al., 2015) with the "glmer.nb" function was used to model this distribution.

I standardized my numerical predictor variables (Total dead wood volume, mean temperature 15cm above ground, mean precipitation, connectivity, and Sciaroidea) by using the "scale" function in R (Becker et al., 1988). They are thus standardized with z-score transformation that gives them a mean of 0 and a variance of 1 (Milligan & Cooper, 1988). The underlying formula for this standardization, as shown in Milligan and Cooper (1988), is $z = \frac{x - \bar{x}}{s}$, where x is an individual data point value of the chosen variable, and $\bar{x}$ and s is the mean and standard deviation of the variable, respectively. Standardization was done to set the variables on a similar, comparable scale (Grueber et al., 2011; Milligan & Cooper, 1988) in addition to address computational issues I encountered during model fitting. My models were not able to converge to a solution without standardization. I backtransformed all the values in my model outputs for interpretation by exponentiating the logarithmic values and reversing the z-score standardization for the standardized values. The formula I used for backtransforming standardized values was: Original variable = (Exponentiated standardized value * Standard deviation of the original variable) + Mean of the original variable.

I followed a model selection procedure to identify which models were best in terms of optimized trade-off between model fit and complexity (Harrison et al., 2018). Candidate models were chosen a priori based on ecological knowledge of which predictor variables that were relevant for each response variable. See Table 1 for my predictor and response variables. I chose to include the subfamily Orthocentrinae due to having data on their hosts, Sciaridae and Mycetophilidae (Broad et al., 2018; Kolarov & Bechev, 1995; Komonen et al., 2000; Quicke, 2015; Roman, 1939; Šedivý & Ševčík, 2003; Shaw & Askew, 2010; Short, 1978; Vilkamaa & Komonen, 2001; Wahl, 1990; Waterston, 1929), both in the superfamily Sciaroidea (Diptera) (Kjærandsen, 2022). This was the only subfamily I had reliable host data for. I made four candidate models for each response variable. Each model followed the same basic setup: Model 1 that includes all the relevant predictor variables, two models (Model 2 and 3) based on Model 1 but with some predictor variables removed, and a null model without any predictor variables but with the random effect (Table 1) (Grueber et al., 2011; Harrison et al., 2018). Models 1 and 2 include site-specific variables that may explain the variation between NN and CC. Model 3 however, focuses more on forest management type without these site-specific variables.

By using Akaike's Information Criterion (AIC) (Akaike, 1973) I could compare and rank competing candidate models and assess which model provides the strongest evidence for explaining the observed data (Harrison et al., 2018; Johnson & Omland, 2004; Tredennick et al., 2021). The models with the lowest AIC were chosen due to being the best models in optimizing the fit and complexity (Harrison et al., 2018; Johnson & Omland, 2004; Richards, 2008). Additionally, I included Model 3 in cases where Model 1 was best, to separate the correlated effect of forest management and dead wood. I annotated p-values <0.05 as significant, but I also added some information about the evidence of the statistical significance of my results, based on (Bland, 1986; Bland, 2015; Muff et al., 2022). These sources use significance based on p-values but explains it with evidence instead of only "significant" and "not significant" (Bland, 1986; Bland, 2015; Muff et al., 2022).

Table 1. Variables used in the four candidate models to explain the response variables abundance of Ichneumonidae, Braconidae, Orthocentrinae, Saproxylic Ichneumonoidea, Specialists, and Generalists. All models included site as a random effect.
Null model: 1+(1|Site_ID)

Predictor variables	**Model 1**	**Model 2**	**Model 3**	**Null model**
Period	X	X	X	
Forest type	X	X	X	
Year	X	X	X	
Mean temperature (°C)	X	X		
Mean precipitation (mm/day)	X	X		
Sciaroidea[a]	X	X		
Dead wood volume (m^3ha^{-1})	X			
Connectivity (m^3ha^{-1})	X			

[a] Only used in models to explain Orthocentrinae (their hosts are Sciaroidea)

3. Results

In total, 1891 wasps from the superfamily Ichneumonoidea were identified, of which 1499 belonged to the family Ichneumonidae (55% in NN), and 392 to the family Braconidae (50% in NN).

As many as 36 subfamilies were identified in the superfamily, of which 31 was found in NN and 32 in CC. Phygadeuontinae were most numerous (323 individuals, 54% in NN) followed by Cryptinae (295 individuals, 74% in NN) (Figure 4). See Appendix 2 for mean number of individuals in each subfamily.

Two new species for Norway were identified:

- *Odontocolon punctulatum* (Thomson) in subfamily Xoridinae, found at Skotjernfjell NN in the third period.
- *Odontocolon longitarsum* (Johansson) in subfamily Xoridinae, found at Tretjerna NN in the third period.

An overview of tribes, genera, and species identified can be found in Appendix 3.

As many as 1055 individuals were grouped as specialists, of which 47% were found in NN. The total number of generalists identified were 809, with 62% in NN. A total of 25 subfamilies of specialists and eight of generalists were found (Appendix 4). Subfamilies of specialists found in NN were 21, compared to 23 in CC. Generalist subfamilies found in NN were seven, compared to seven in CC.

The number of saproxylic Ichneumonoidea identified were 661 (58% in NN), and the number of saproxylic subfamilies were 11 (Appendix 4). Saproxylic subfamilies in NN were 10, compared to 10 in CC.

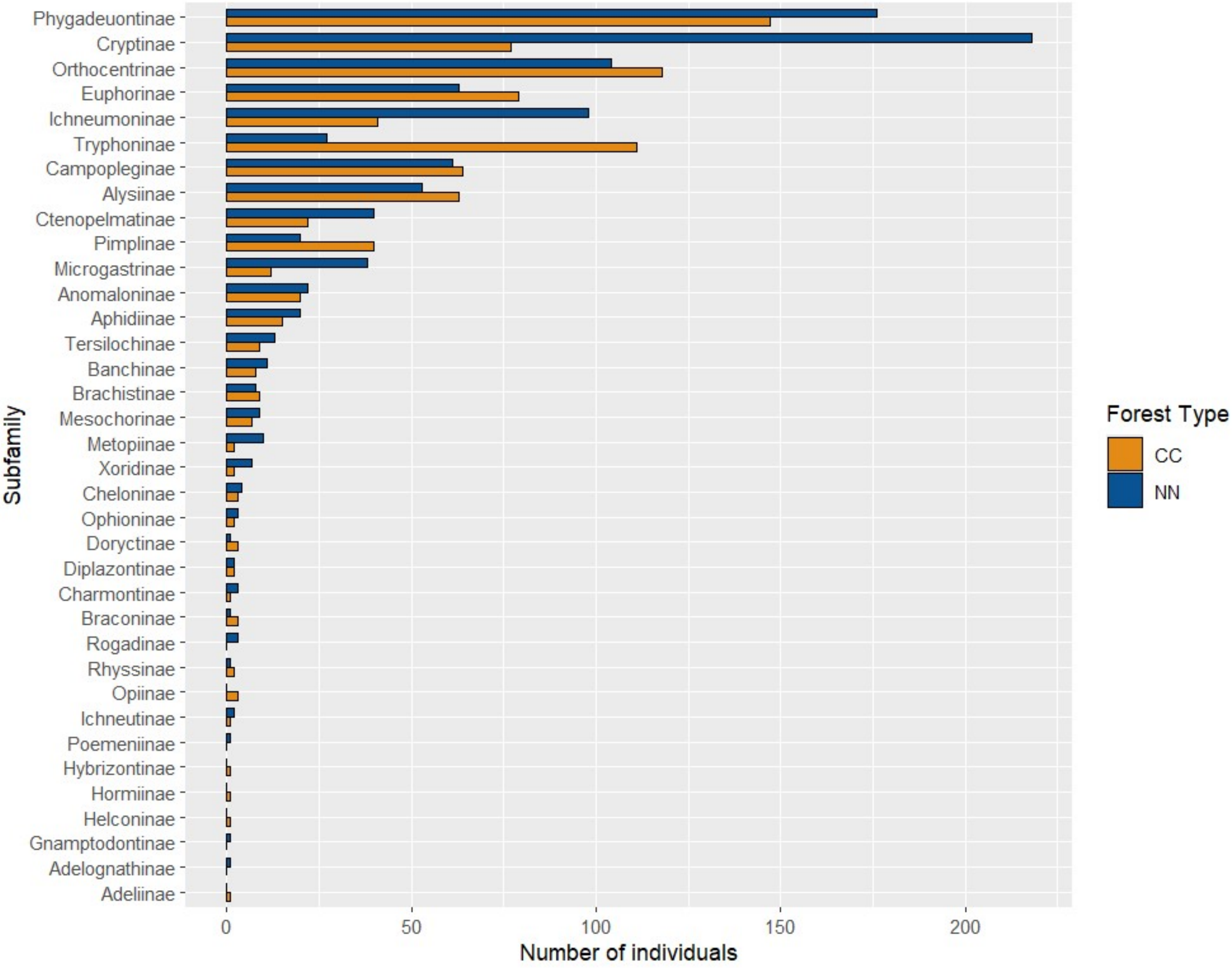

Figure 4. Total number of individuals identified per subfamily, sorted by descending abundance. The two forest management types are treated separately. (CC= former clear cut, NN= near natural).

3.1 Abundance of Ichneumonoidea between the forest management types

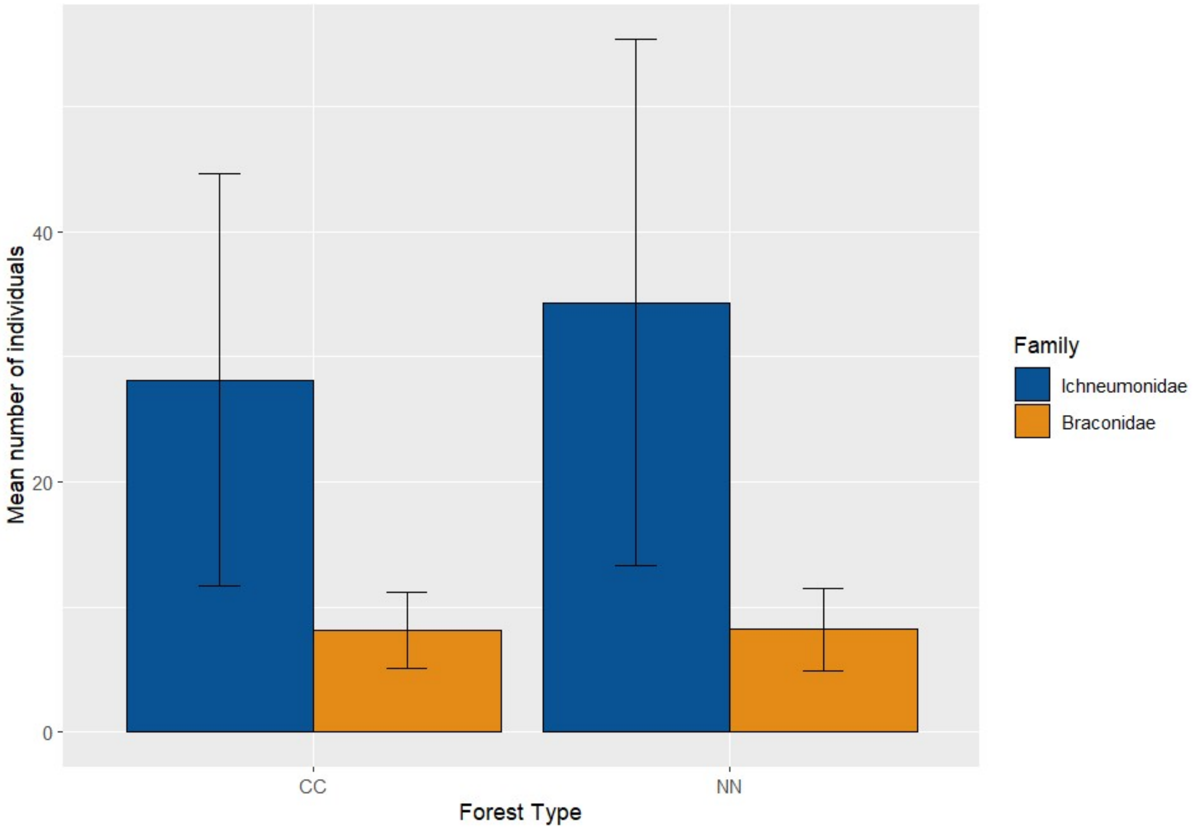

Figure 5. Mean number of individuals in each family of Ichneumonoidea between the forest management types. Error bars indicate the 95% confidence interval around the mean (+2 SE (Standard error)). (CC= former clear cut, NN= near natural).

3.1.1 Ichneumonidae

Forest management did not have a significant effect on the abundance of Ichneumonidae when including design variables only (Model 3, Appendix 5, Figure 5). The best model was the model containing all the predictor variables (Model 1, Table 2). In contrast to forest management, the volume of dead wood had a significant effect. There was strong evidence for an increase in Ichneumonidae with an increase in the volume of dead wood (p=0.005) (Table 2, Figure 6). According to the best model, for each one unit increase in dead wood volume, the expected number of Ichneumonidae increased by approximately 102 times (Table 2). Sampling period and mean temperature did also significantly affect the abundance of Ichneumonidae, with very strong evidence (p <0.001), and evidence (p= 0.042) respectively (Table 2). According to the best model, approximately 15 times as many Ichneumonidae were expected in period 3 compared to period 1, and for each one degree increase in mean temperature the expected number of Ichneumonidae decreased by approximately 15 times (Table 2).

Table 2. Optimal generalized linear mixed model of the abundance of Ichneumonidae (Model 1). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	1.300 (3.670)	0.299	4.353	**<0.001**
Period (3)	2.738 (15.462)	0.509	5.384	**<0.001**
Year (2023)	1.617 (5.038)	0.379	4.270	**<0.001**
Forest type (NN)	-0.353 (0.703)	0.239	-1.477	0.140
Dead wood volume	0.381 (102.105)	0.135	2.812	**0.005**
Mean temperature	-0.478 (14.813)	0.235	-2.032	**0.042**
Mean precipitation	0.286 (6.968)	0.166	1.725	0.084
Connectivity	0.053 (535803.821)	0.135	0.394	0.694

The random effect Site_ID has an estimated variance close to zero ($2.77e^{-15}$).

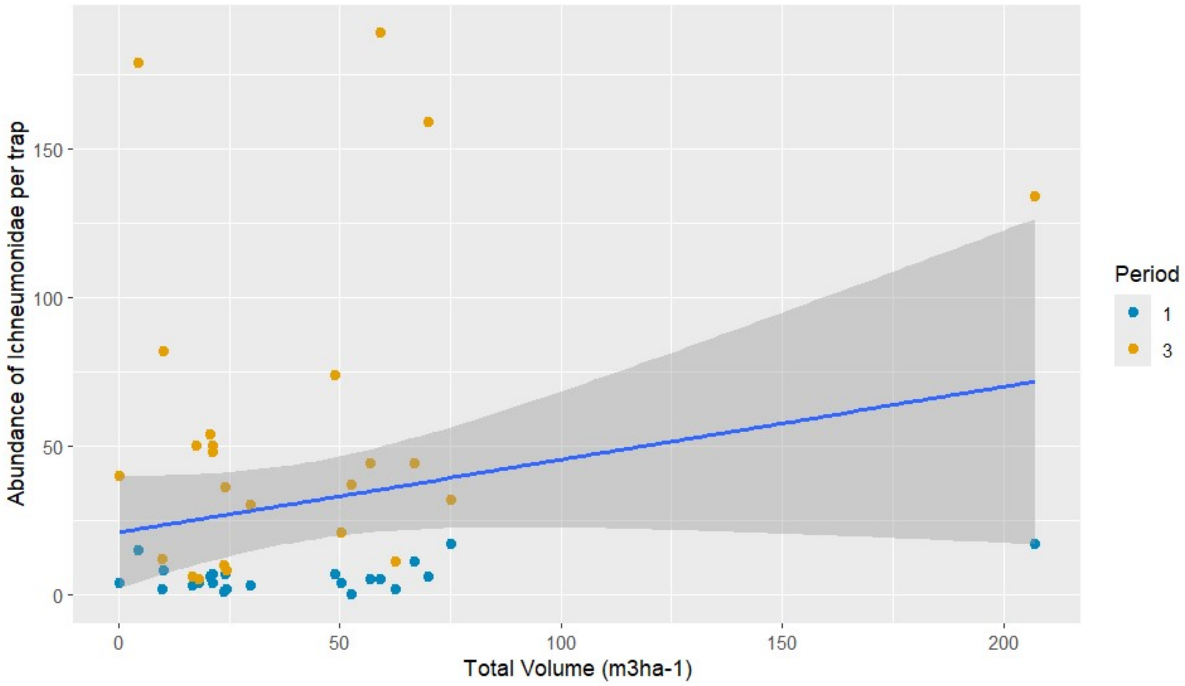

Figure 6. Abundance of Ichneumonidae per trap compared to the total volume of dead wood at each site. Each dot corresponds to a trap at each site. The data for total volume of dead wood are original and non-standardized. Regression line fitted with a 95% confidence interval.

3.1.2 Braconidae

Forest management did not affect the abundance of Braconidae significantly (Model 3, Table 3, Figure 5). Similarly to Ichneumonidae, there was very strong evidence for a greater number of Braconidae in period 3 compared to period 1 (p <0.001) (Table 3). According to the best model, approximately 3 times as many Braconidae were expected in period 3 compared to period 1 (Table 3).

Table 3. Optimal generalized linear mixed model of the abundance of Braconidae (Model 3). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	1.367 (3.925)	0.257	5.325	**<0.001**
Period (3)	1.129 (3.091)	0.257	4.391	**<0.001**
Year (2023)	0.113 (1.120)	0.418	0.271	0.786
Forest type (NN)	-0.130 (0.878)	0.252	-0.516	0.606

3.1.3 Orthocentrinae

Forest management did not have a significant effect on the abundance of Orthocentrinae when including design variables only (Model 3, Appendix 6, Figure 7). Forest management did however significantly affect the number of Orthocentrinae in the best model, with evidence for a decrease in NN compared to CC (p=0.015) (Model 1, Table 4, Figure 7). According to the best model, the expected number of Orthocentrinae in NN was approximately 40.8% of the expected number in CC (Table 4). The volume of dead wood had a significant effect on Orthocentrinae. There was strong evidence for an increase in Orthocentrinae with an increase in the volume of dead wood (p=0.005) (Table 4, Figure 8). According to the best model, for each one unit increase in dead wood volume, the expected number of Orthocentrinae increased by approximately 109 times (Table 4). There was also strong evidence for a greater number of Orthocentrinae in period 3 compared to period 1 (p=0.007), and according to the best model approximately 8 times as many Orthocentrinae were expected in period 3 compared to period 1 (Table 4). The rest of the predictor variables in Table 4 had no significant effect on the abundance of Orthocentrinae.

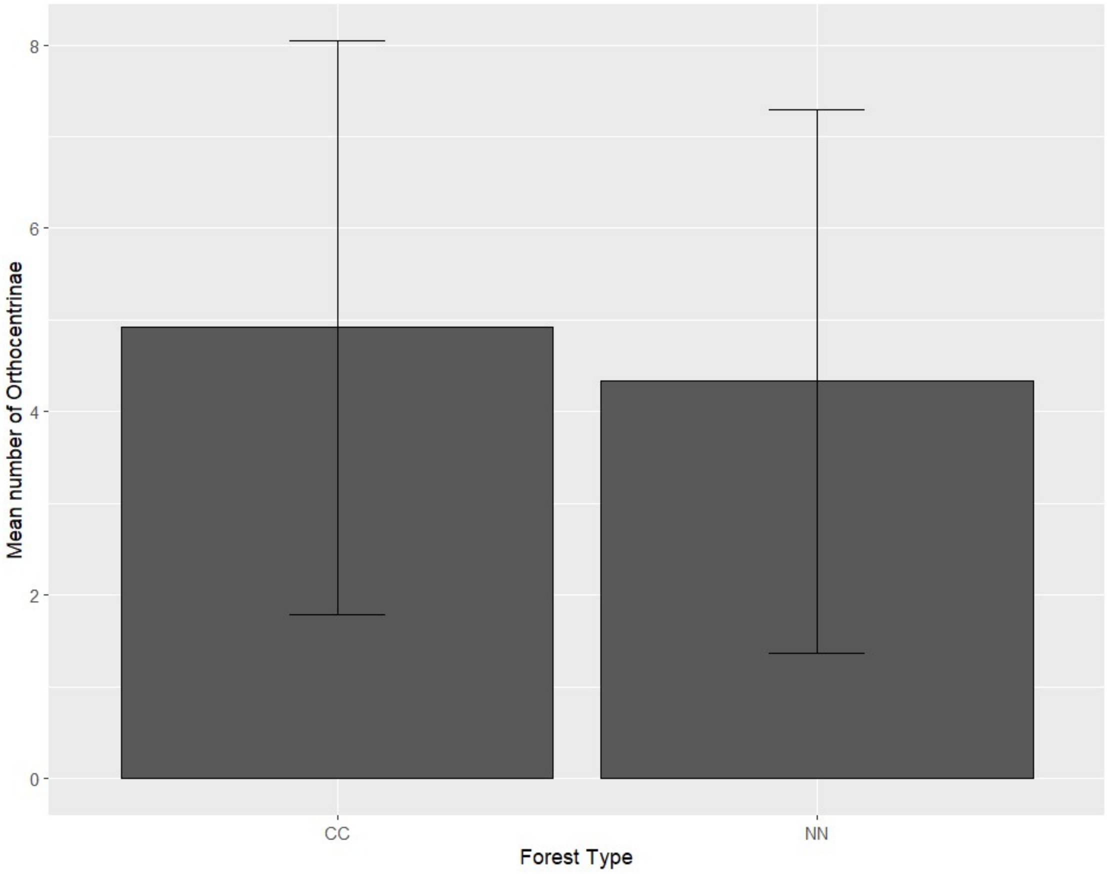

Figure 7. Mean number of Orthocentrinae between the forest management types. Error bars indicate the 95% confidence interval around the mean (+2 SE (Standard error)). (CC= former clear cut, NN= near natural).

Table 4. Optimal generalized linear mixed model of the abundance of Orthocentrinae (Model 1). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	0.073 (1.076)	0.474	0.154	0.877
Period (3)	2.039 (7.686)	0.753	2.709	**0.007**
Year (2023)	0.296 (1.344)	0.514	0.575	0.565
Forest type (NN)	-0.897 (0.408)	0.369	-2.430	**0.015**
Dead wood volume	0.488 (108.983)	0.175	2.787	**0.005**
Sciaroidea	-0.294 (700.735)	0.315	-0.934	0.350
Mean temperature	0.064 (16.677)	0.351	0.182	0.855
Mean precipitation	0.130 (6.529)	0.204	0.639	0.523
Connectivity	0.139 (548271.537)	0.196	0.712	0.477

The random effect Site_ID has an estimated variance close to zero ($1.699e^{-14}$).

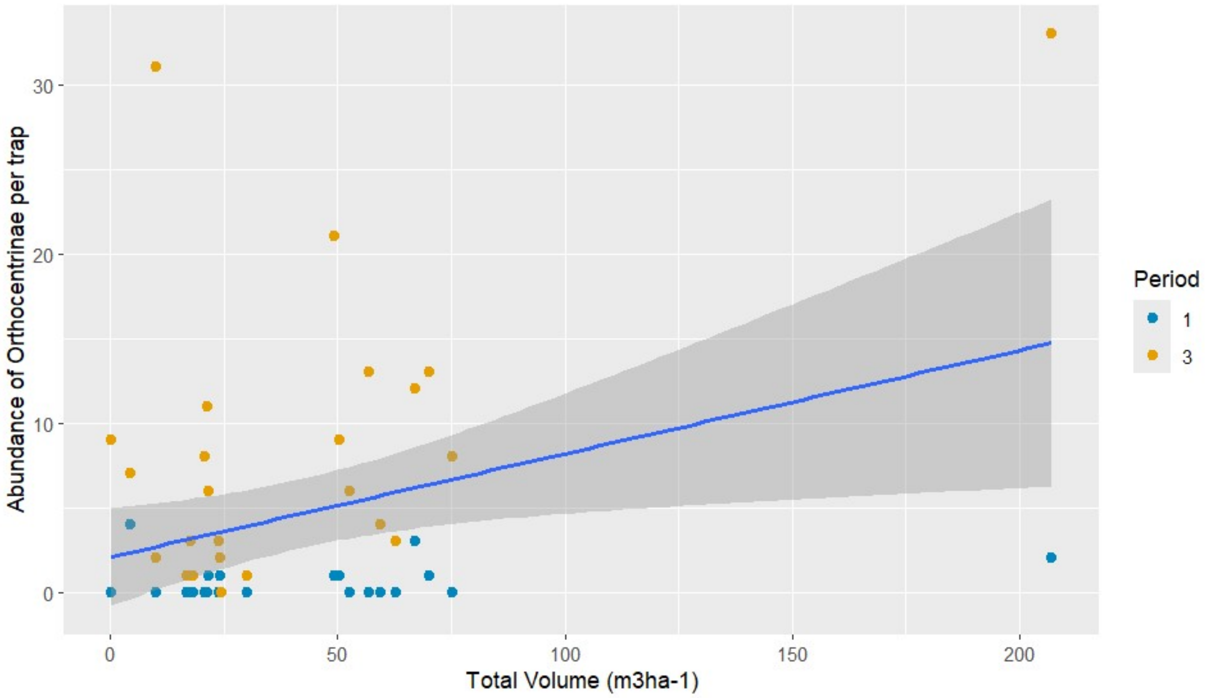

Figure 8. Abundance of Orthocentrinae per trap compared to the total volume of dead wood at each site. Each dot corresponds to a trap at each site. The data for total volume of dead wood are original and non-standardized. Regression line fitted with a 95% confidence interval.

3.1.4 Top five most abundant subfamilies (excluding Orthocentrinae)

Forest management significantly affected the abundance of the subfamilies Cryptinae and Ichneumoninae, both showing evidence for an increase in NN compared to CC (Table 5, Appendix 7, Appendix 8). The volume of dead wood did not significantly affect any of the subfamilies (Table 5, Appendix 7-11). Sampling period significantly affected all subfamilies except Euphorinae, with strong evidence for an increase in their numbers in period 3 compared to period 1 (Table 5, Appendix 7-11). Mean temperature had a significant negative effect on Ichneumoninae and Tryphoninae, both showing evidence for a decrease when temperature increased (Table 5, Appendix 8, Appendix 9). Mean precipitation had a significant positive effect on Cryptinae and Ichneumoninae, and there was evidence for an increase in their numbers with an increase in precipitation (Table 5, Appendix 7, Appendix 8). Connectivity was only significant for Phygadeuontinae, showing evidence for an increase in its numbers with an increase in connectivity of old forest habitat (Table 5, Appendix 10).

Table 5. Summary of the predictor variables for the five most abundant subfamilies (excluding Orthocentrinae). The strength of evidence for the significant ($p<0.05$) variables are included. Positive significant relationships are annotated as "+" and negative significant relationships as "–". A positive significant relationship for forest management implies a greater number of individuals in NN compared to CC (NN>CC), while the opposite is implied for negative significant relationships (CC>NN). If the variable is not included in the model, it is annotated as "not included". Details can be found in Appendix 7-11.

Subfamily	**Forest management**	**Dead wood**	**Period**	**Mean temperature**	**Mean precipitation**	**Connectivity**
Phygadeuontinae (Model 1)	Not significant for Model 1 or Model 3.	Not significant	Significant + (Strong evidence)	Not significant	Not significant	Significant + (Evidence)
Cryptinae (Model 2)	Significant + (Evidence) NN>CC	Not included	Significant + (Strong evidence)	Not significant	Significant + (Evidence)	Not included
Euphorinae (Null model)	Not included	Not included	Not included	Not included	Not included	Not included
Ichneumoninae (Model 2)	Significant + (Evidence) NN>CC	Not included	Significant + (Strong evidence)	Significant – (Evidence)	Significant + (Evidence)	Not included
Tryphoninae (Model 2)*	Not significant	Not included	Significant + (Strong evidence)	Significant – (Evidence)	Not significant	Not included
*Tryphoninae Model 1 had lower AIC but reached its iteration limit, suggesting that it may not be a good fit. This is why the next best model, Model 2, was chosen.						

3.2 Specialist and generalist Ichneumonoidea

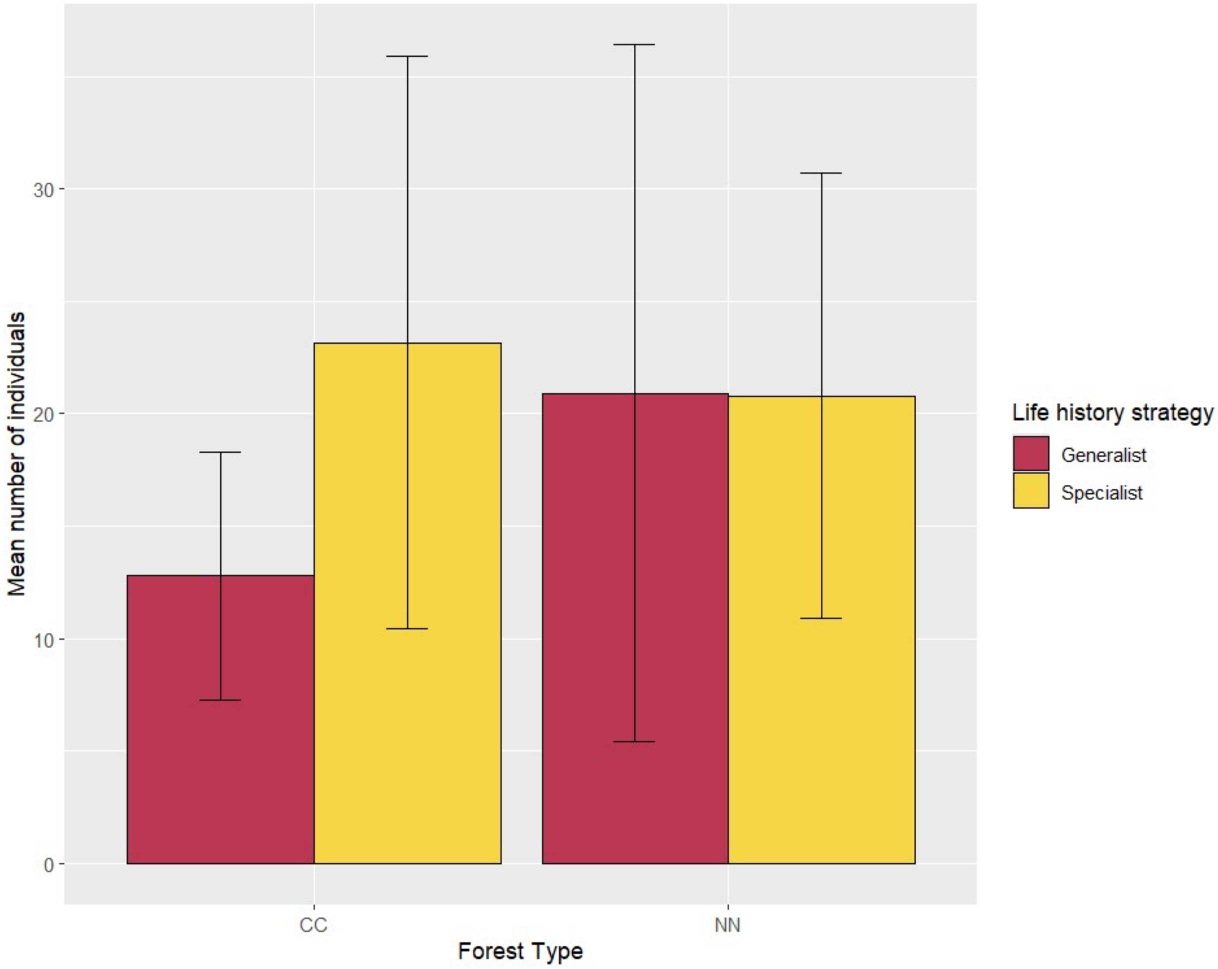

Figure 9. Mean number of specialist and generalist Ichneumonoidea between the forest management types. Error bars indicate the 95% confidence interval around the mean (+2 SE (Standard error)). (CC= former clear cut, NN= near natural).

3.2.1 Specialists

Forest management did not significantly affect the abundance of specialists (Model 3, Table 6, Figure 9). There was very strong evidence for a greater number of specialists in period 3 compared to period 1 (p <0.001) (Table 6). According to the best model, approximately 7 times as many specialists were expected in period 3 compared to period 1 (Table 6).

Table 6. Optimal generalized linear mixed model of the abundance of specialists (Model 3). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	1.664 (5.283)	0.226	7.375	**<0.001**
Period (3)	1.914 (6.778)	0.226	8.458	**<0.001**
Year (2023)	0.482 (1.619)	0.348	1.384	0.166
Forest type (NN)	-0.160 (0.852)	0.228	-0.705	0.481

3.2.2 Generalists

Forest management did not have a significant effect on the abundance of generalists when including design variables only (Model 3, Appendix 12, Figure 9). The best model was the model containing all the predictor variables (Model 1, Table 7). In contrast to specialists, there was evidence for an increase in generalists with an increase in the volume of dead wood (p=0.020) (Table 7, Figure 10). According to the best model, for each one unit increase in dead wood volume, the expected number of generalists increased by approximately 101 times (Table 7). There was very strong evidence for a greater number of generalists in period 3 compared to period 1 (p <0.001) (Table 7). Approximately 10 times as many generalists were expected in period 3 compared to period 1 according to the best model (Table 7). While there was evidence for an increase in generalists with an increase in mean precipitation (p=0.032), generalists showed evidence for a decrease with an increase in mean temperature (p=0.035) (Table 7). The best model predicted that for each one unit increase in mean precipitation, the expected number of generalists increased by approximately 7 times (Table 7). It also predicted that for each one degree increase in mean temperature the expected number of generalists decreased by approximately 15 times (Table 7).

Table 7. Optimal generalized linear mixed model of the abundance of generalists (Model 1). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	0.999 (2.717)	0.337	2.966	**0.003**
Period (3)	2.297 (9.940)	0.567	4.051	**<0.001**
Year (2023)	1.561 (4.763)	0.418	3.736	**<0.001**
Forest type (NN)	-0.301 (0.740)	0.276	-1.089	0.276
Dead wood volume	0.363 (101.033)	0.156	2.328	**0.020**
Mean temperature	-0.562 (14.604)	0.266	-2.113	**0.035**
Mean precipitation	0.388 (7.296)	0.181	2.150	**0.032**
Connectivity	0.148 (549616.201)	0.147	1.005	0.315

The random effect Site_ID has an estimated variance close to zero ($2.158e^{-11}$).

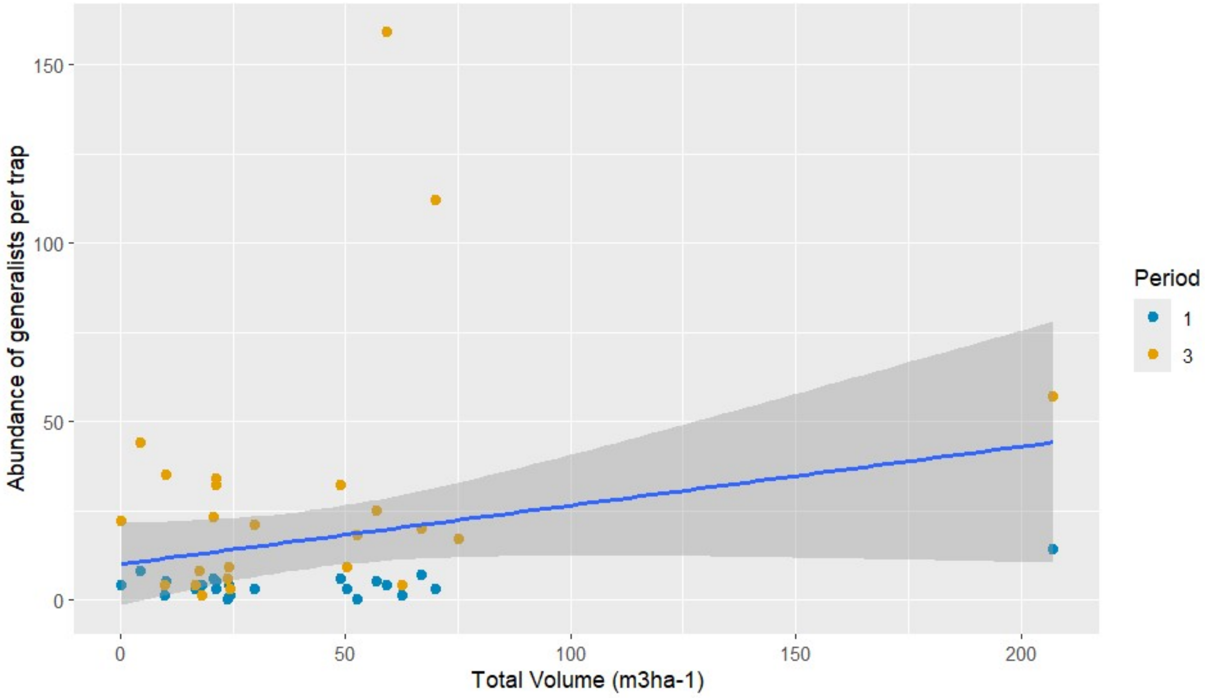

Figure 10. Abundance of generalists per trap compared to the total volume of dead wood at each site. Each dot corresponds to a trap at each site. The data for total volume of dead wood are original and non-standardized. Regression line fitted with a 95% confidence interval.

3.3 Saproxylic Ichneumonoidea

Forest management and dead wood volume did not significantly affect the abundance of saproxylic Ichneumonoidea (Model 2, Table 8, Figure 11). There was evidence for an increase in saproxylic Ichneumonoidea with an increase in mean precipitation (p=0.027) (Table 8). According to the best model, for each one unit increase in mean precipitation, the expected number of saproxylic Ichneumonoidea increased by approximately 8 times (Table 8). The rest of the predictor variables in Table 8 had no significant effect on the abundance of saproxylic Ichneumonoidea. See Appendix 13 for mean number of saproxylic Ichneumonoidea across the different sites.

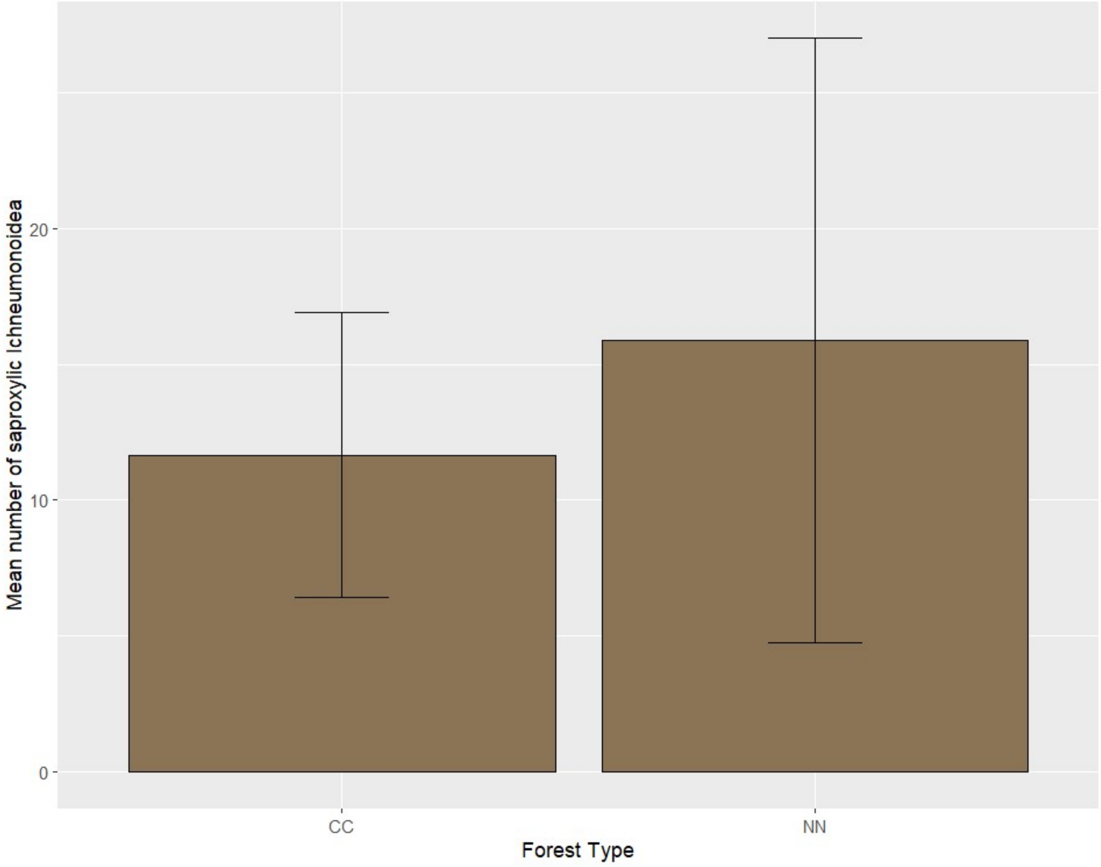

Figure 11. Mean number of saproxylic Ichneumonoidea between the forest management types. Error bars indicate the 95% confidence interval around the mean (+2 SE (Standard error)). (CC= former clear cut, NN= near natural).

Table 8. Optimal generalized linear mixed model of the abundance of saproxylic Ichneumonoidea (Model 2). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	**Estimate**	**SE**	**z-value**	**p-value**
Intercept	1.602 (4.964)	0.403	3.973	**<0.001**
Period (3)	0.654 (1.922)	0.693	0.944	0.345
Year (2023)	0.971 (2.640)	0.612	1.586	0.113
Forest type (NN)	0.108 (1.114)	0.294	0.366	0.715
Mean temperature	0.299 (17.860)	0.358	0.837	0.403
Mean precipitation	0.520 (7.769)	0.236	2.205	**0.027**

4. Discussion

In this master project, I have investigated the long-term effects of forest management on the abundance of the parasitoid superfamily Ichneumonoidea. I expected that the abundance of Ichneumonoid families and subfamilies were greater in NN sites compared to CC sites. Additionally, I expected NN to contain a greater abundance of specialists (koinobionts) compared to generalists (idiobionts), and thus that the effect of forest management was affecting specialists more than generalists. Furthermore, I anticipated that the abundance of saproxylic Ichneumonoidea were greater in NN sites compared to CC sites, particularly in areas with a larger volume of dead wood.

4.1 Forest management effects on the abundance of Ichneumonoidea

I did not find evidence for a difference in the abundance of any of the families between the forest management types. However, there were differences among the subfamilies. This was partly in accordance with my first prediction that expected a greater abundance in NN compared to CC.

The lack of difference on the family level could be due to the diversity of different subfamilies within each family, with slightly different life histories and host relationships (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015). Some subfamilies may be more abundant in NN and others in CC, thereby hiding a clear pattern of evidence for one forest management type being favorable over the other at the family level. This is evident for the subfamilies Orthocentrinae, Cryptinae, and Ichneumoninae. Orthocentrinae had evidence for a decrease in abundance in NN compared to CC, while Cryptinae and Ichneumoninae had evidence for an increase in NN compared to CC. Forest management did however not show any significant effect for Orthocentrinae when dead wood and other environmental variables were removed, meaning that the effect of forest management on Orthocentrinae may not be as impactful as indicated by the best model.

Each subfamily may respond differently to disturbances in the landscape. Given the time since clear-cutting (1940's-1960's), it could be possible that individuals from both families and many of their subfamilies have recolonized or dispersed into the clear-cut forest from nearby near-natural sites (Gibb et al., 2008; Paillet et al., 2010). That is if they disappeared in the first place, which remains unknown. The near-natural forests could also be influenced by the managed forests around them (Paillet et al., 2010), meaning that subfamilies present in CC may colonize NN as well, thereby decreasing the difference between them.

The dispersal distances of parasitoid wasps can vary considerably, with some dispersing poorly and others dispersing greater distances in relation to their hosts (Couchoux et al., 2016; Cronin & Reeve, 2005; Gibb et al., 2008; Hilszczański, 2018; Jonsell et al., 1999; Komonen et al., 2000). Some arthropod predators have used 60-80 years to recover to similar levels as before clear-cutting (Niemelä, 1999; Niemelä et al., 1996). This shows that there is potential for recovery after enough time has passed, even though other arthropods like Mycetophilidae (Diptera), one of the hosts of Orthocentrinae (Broad et al., 2018; Kolarov & Bechev, 1995; Quicke, 2015; Šedivý & Ševčík, 2003; Shaw & Askew, 2010; Short, 1978; Wahl, 1990), may not recover equally well (Økland, 1994).

Clear-cut forest may mimic natural fire disturbance in boreal forests (Paillet et al., 2010; Pedlar et al., 2002), and if the native tree species remain after clear-cutting, the difference in species richness between clear-cut forest and unmanaged forests may not be as significant as if the tree species had been replaced (Paillet et al., 2010). The intensity and frequency of clear-cutting as well as the amount of dead wood remaining may however differ from natural fire disturbance and lead to different ecological effects (Niemelä, 1999; Niemelä et al., 2007;

Paillet et al., 2010; Pedlar et al., 2002; Stokland et al., 2012; Toivanen & Kotiaho, 2007). The tree species in my study were not replaced after clear-cutting, but a question for future studies could be if a greater difference between the forest management types appears after multiple clear-cuttings.

Studies have had a focus on the difference between relatively recent clear-cut forest and mature managed (selective felling) or old growth forest (Gibb et al., 2008; Hilszczański et al., 2005; Komonen et al., 2000; Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010) leaving out the long-term effects of clear-cutting on parasitoid wasps. Komonen et al. (2000) conducted a study in spruce swamp forests in eastern Finland and found that parasitoids were missing from old-growth forest fragments that have had their surroundings clear-cut 12-32 years ago. Extinctions of lower trophic levels and limited dispersal ability are suggested reasons for this finding (Komonen et al., 2000). Other studies have focused more on saproxylic Ichneumonoidea in particular and will be discussed in chapter 4.3.

Keys for the identification of Ichneumonoidea have in recent years become comprehensive, at least for subfamilies (e.g., Broad et al., 2018; Hackston, 2024). However, determining down to species level is still difficult and time consuming, and in many cases the hosts remain unknown (Broad et al., 2018; Quicke, 2015). Comparing abundance at the species level could have provided a more detailed difference in Ichneumonoidea between the forest management types, but this was beyond the scope of my thesis.

4.2 Specialist and generalist Ichneumonoidea

I did not find evidence for a difference in the abundance of specialist and generalist Ichneumonoidea between the forest management types. This was not in accordance with my second prediction that expected a greater abundance of specialists in NN. However, I did expect that there would be less of a difference between the forest management types for generalists.

It has been suggested that the most specialized species in higher trophic levels are vulnerable to extinction when exposed to a forest landscape with a history of clear-cutting (Komonen et al., 2000). A study by Hilszczański et al. (2005) in northern Sweden's boreal spruce forest found that specialists (koinobionts) were less abundant in the recent clear-cut forest (cut 1-3 years prior) compared to old growth forest reserves (mean age of 151 years) and mature managed forest (mean age of 108 years), while the opposite was true for generalists (idiobionts) (Hilszczański et al., 2005). Stenbacka, Hjältén, Hilszczański, Ball, et al. (2010) also conducted a study in the northern boreal forests of Sweden and found the same pattern for koinobionts and idiobionts in forest stands of the same age as Hilszczański et al. (2005). Idiobionts preferred recent clear-cuts while koinobionts preferred mature managed forests and old-growth reserves (Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010).

Koinobiont and idiobiont are specific life history strategies (Askew & Shaw, 1986), and in reality, parasitoids may not follow these ideal ends equally (Quicke, 2015). Koinobionts are often regarded as specialist parasitizing one or a few hosts and idiobionts as generalist parasitizing a greater range of hosts (Althoff, 2003; Askew & Shaw, 1986; Broad et al., 2018; Fitton et al., 1988; Hilszczański, 2018; Quicke, 2015), but studies have often neglected host ranges at the species level, and host records are not always reliable (Hilszczański, 2018; Quicke, 2015; Shaw, 2017). Some parasitoid subfamilies even have specific taxa as their hosts regardless of life history strategy, like Ichneumoninae (both koinobiont and idiobiont) that only parasitize Lepidoptera (Broad et al., 2018; Godfray, 1994).

The way the immature parasitoid feed on its host, including if the host is exposed or concealed may be important clues regarding how specialized the parasitoid is (Godfray, 1994; Hilszczański, 2018; Quicke, 2015). Endoparasitoids have to overcome the host immune responses, but can be safer from possible external attacks from the host and from predators and hyperparasitoids (Gauld, 1988; Godfray, 1994; Quicke, 2015). This means that they may have a greater chance of survival on exposed hosts than ectoparasitoids (Gauld, 1988; Hawkins, 1990; Hawkins et al., 1992; Quicke, 2015). Ectoparasitoids relies on finding a concealed host to avoid being attacked by predators or hyperparasitoids, and they often need to paralyze the host to avoid being dislodged or squashed by it (Gauld, 1988; Hawkins, 1990; Hawkins et al., 1992; Quicke, 2015).

Most koinobionts are endoparasitoids, and most idiobionts are ectoparasitoids, but there are exceptions (Broad et al., 2018; Quicke, 2015). Tryphoninae, and the *Polysphincta* group of Pimplinae are koinobiont ectoparasitoids that are specialized to attach to their host (Broad et al., 2018; Eberhard, 2000; Fitton et al., 1988; Gauld & Dubois, 2006; Gauld et al., 2002; Godfray, 1994; Korenko et al., 2022; Matsumoto, 2016; Quicke, 2015; Weng & Barrantes, 2007). Due to being koinobionts, these were accounted for in my samples. It is less clear how specialized the idiobiont endoparasitoids are, but it is possible that the host range may still be wider than the koinobiont endoparasitoids at least at the species level for the subfamily Ichneumoninae and Pimplinae (Broad et al., 2018).

Some idiobiont ectoparasitoids like Rhyssinae specialize on locating hosts deep within wood, meaning that even though they are idiobiont ectoparasitoids capable of parasitizing different hosts, they are still specialized (Broad et al., 2018; Chrystal & Skinner, 1931; Fitton et al., 1988; Gauld et al., 2002; Hanson, 1939; Hilszczański, 2018; Madden, 1968; Quicke, 2015; Quicke et al., 2009; Shaw, 2006; Spradbery, 1970a, 1970b; Wahl & Gauld, 1998). The idiobiont ectoparasitoid genus *Scambus* (Pimplinae) may even be niche specialists (Broad et al., 2018; Fitton et al., 1988). Such degree of specialization for idiobionts were not considered in my samples when I categorized them into specialist or generalist. I cannot exclude the possibility that this type of specialization for idiobionts may occur for multiple other subfamilies at the species level in my samples.

Koinobionts may attack multiple hosts, and some koinobiont endoparasitoids with more than one generation per year, attacking different hosts in each of their generations (Althoff, 2003; Broad et al., 2018; Hilszczański, 2018; Quicke, 2015; Shaw & Huddleston, 1991; Shaw et al., 2016). According to Hilszczański (2018), 14 cerambycid (Cerambycidae) hosts have been found for *Helcon tardator* Nees (Helconinae), a koinobiont in the family Braconidae (Hilszczański, 2018). Only one *Helcon tardator* were found in my samples (Appendix 3), but there could potentially be more species that follow the same pattern (Althoff, 2003; Broad et al., 2018; Hilszczański, 2018; Quicke, 2015; Shaw & Huddleston, 1991; Shaw et al., 2016). Due to differing strategies at the species level, it may be difficult to say for certain which so called “specialist” subfamily truly depend on each forest management type for survival.

4.3 Forest management effects on the abundance of saproxylic Ichneumonoidea

I did not find evidence for a difference in the abundance of saproxylic Ichneumonoidea between the forest management types. This was not in accordance with my third prediction that expected a greater abundance in NN compared to CC.

Hilszczański et al. (2005) found that forest management type significantly affected the assemblage of saproxylic beetle associated Ichneumonoidea. There was a difference at the species level between the recent clear-cut forest, mature managed forest, and old growth forest (Hilszczański et al., 2005) as mentioned in chapter 4.2. Stenbacka, Hjältén, Hilszczański, Ball, et al. (2010) did not find any significant difference in total abundance of saproxylic Ichneumonoidea between the forest management types but did find a significant effect on the koinobionts and idiobionts discussed in chapter 4.2. None of the forest stands had a complete saproxylic parasitoid assemblage, which means that the whole range of forest management types, from clear-cuts to old-growth forest, may be needed to support the whole parasitoid community (Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010).

Some subfamilies, regardless of being saproxylic or not, only occurred in NN, and others only in CC in my samples. This may indicate that the forest management types support slightly different assemblages. However, I did not test if there was a difference in composition or assemblages of the parasitoid wasps between the forest management types. Additionally, the number of individuals within the subfamilies unique to each forest management type was extremely low (1-3 individuals), which may indicate that the observed difference could be attributable to random variation.

My categorization of saproxylic subfamilies may have been too broad. Saproxylic subfamilies in my samples contain both saproxylic and partly saproxylic subfamilies. This was due to the very limited amount of potentially "fully saproxylic" subfamilies in my samples (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015). The saproxylic category could therefore include many species that are not strictly dependent on dead wood. This may be an important reason for not finding evidence for a difference in saproxylic Ichneumonoidea between the forest management types. Conversely, even though Hilszczański (2018) made an overview of the subfamilies that are known to have saproxylic species, there could potentially be other subfamilies containing saproxylic species that has not been studied yet. At least since there is still knowledge gaps on hosts records (Broad et al., 2018; Quicke, 2015). This remain unknown, as far as I know, and could be a topic for future studies.

4.4 Dead wood volume effects on Ichneumonoidea

Ichneumonidae and Orthocentrinae had strong evidence, and generalists had evidence for an increase in their abundance with the increase of total volume of dead wood. None of the other response variables had any evidence for an effect with total volume. This was not directly in accordance with my fourth prediction that expected a greater abundance of saproxylic Ichneumonoidea with greater volume of dead wood.

The increase in the abundance of Ichneumonidae and generalists with a greater volume of dead wood is likely due to the importance of dead wood as habitat for many of their hosts (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015). Several subfamilies within Ichneumonidae are saproxylic, which makes Ichneumonidae partly saproxylic in itself

(Hilszczański, 2018). Similarly, several of the saproxylic subfamilies within Ichneumonidae are comprised of generalists (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015). Hilszczański (2018) did not include Orthocentrinae as saproxylic, even though they parasitize Mycetophilidae and Sciaridae (Broad et al., 2018; Kolarov & Bechev, 1995; Komonen et al., 2000; Quicke, 2015; Roman, 1939; Šedivý & Ševčík, 2003; Shaw & Askew, 2010; Short, 1978; Vilkamaa & Komonen, 2001; Wahl, 1990; Waterston, 1929) which are known to have a connection to rotting wood (Ulyshen, 2018). This means that even though Orthocentrinae itself may not be saproxylic, it could be that forests with a large volume of rotting wood may contribute indirectly to increasing their numbers through their hosts. I did however not find any effect of Sciaroidea on Orthocentrinae, and Mycetophilidae may not be dependent on dead wood volume alone, with other factors like continuity of their suitable forest habitat playing an important role (Økland, 1994, 1996). This makes it difficult to draw any conclusions.

I expected a stronger effect of total volume of dead wood for saproxylic Ichneumonoidea per se. The lack of evidence for the other response variables could be due to several reasons. Some saproxylic Braconidae may be abundant on young and thin wood (Jonsell et al., 2023). Jonsell et al. (2023) suggested that this could be due to parasitizing bark beetles which has been known to occur in such wood (Jonsell, 2008; Jonsell et al., 2023). Both species of Braconidae used in the analysis of Jonsell et al. (2023) were in the subfamily Doryctinae, and I only found four individuals of those in my samples (Appendix 4). I cannot conclude if the findings in Jonsell et al. (2023) apply to any of my sampled subfamilies, but it shows that for at least some species, larger diameter dead wood and thus larger volume may not always be the most favorable (Jonsell et al., 2023).

Gibb et al. (2008) found that the volume of dead wood at a local scale (within 100 m of their sites) could be of limited importance for saproxylic beetle associated Ichneumonoidea, and that those parasitoids would not find their hosts easier in these areas with higher dead wood volume. They only used early decay stages of dead wood in their analyses, and suggested that the result could have something to do with the possible high dispersal ability of the beetle hosts associated with early decay stages, which would limit their dependence on the dead wood locally (Forsse & Solbreck, 1985; Gibb et al., 2008; Nilssen, 1984).

Variation of dead wood types/posture could be important for saproxylic Ichneumonoidea with studies showing that standing dead wood supports a different and usually greater number of parasitoids than downed dead wood (Hilszczański, 2018; Hilszczański et al., 2005; Ulyshen et al., 2011). Additionally, high stumps may support a higher density of some parasitoid species compared to low stumps (Hedgren, 2007). Hilszczański et al. (2005) found that a diversity of dead wood substrates is needed to support a more completed saproxylic beetle associated parasitoid assemblage (Hilszczański et al., 2005). Tests for standing and downed dead wood was not included in my study due to being correlated. I thus combined standing and downed dead wood to investigate whether parasitoid wasps were affected by the total volume of dead wood.

The volume of dead wood per se may not give a complete explanation for all the varying effects of dead wood on Ichneumonoidea. The decay stages of dead wood may also be important, and thus the real effect of dead wood on the abundance of Ichneumonoidea may be more complex, with certain species being more abundant in specific decay stages (Siitonen, 2001; Stenbacka, Hjältén, Hilszczański, & Dynesius, 2010; Stokland et al., 2012; Storaunet et al., 2005). Testing this was beyond the scope of my thesis, and future studies should consider examining the effects of different dead wood types and decay stages on parasitoid wasps in greater detail.

4.5 Environmental variables

There was an increase in the abundance of most Ichneumonoidea in period 3 (July, mean temperature: 15.8 °C) compared to period 1 (June, mean temperature: 8.7 °C). July and August have been regarded as the main flight season for Hymenoptera with Ichneumonidae having peaks around August (Fraser et al., 2007; Owen, 1991). Similar to my findings, Stenbacka, Hjältén, Hilszczański, Ball, et al. (2010) also found a greater number of parasitoids in July compared to June. They did however not find any koinobionts in June (Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010), which is different from my samples that found both koinobiont and idiobiont individuals in both periods (Appendix 3, Appendix 4).

In temperate regions, many Ichneumonoidea may synchronize overwintering or diapause emergence with their hosts, and respond to cues like photoperiod, host conditions and temperature (Hance et al., 2007; Quicke, 2015). Temperature could possibly be a limiting factor for the availability of nectar and hosts for the parasitoids early in the season (Gibb et al., 2008), and may affect the host-parasitoid phenological synchrony (Dyer et al., 2013; Hance et al., 2007; Jeffs & Lewis, 2013).

Parasitoids that eat as adults may depend on nectar, honeydew, or host hemolymph for survival and egg maturation (Godfray, 1994; Quicke, 2015; Russell, 2015), meaning that if those food sources, and available hosts, are scarce early in the season and increase later due to temperature (Dyer et al., 2013; Gibb et al., 2008; Hance et al., 2007; Jeffs & Lewis, 2013), it may affect the abundance of parasitoids in the different periods. Testing this was not part of my study and the degree of dependence upon these food sources among my samples remain unknown.

My results suggest that as the temperature increases, Ichneumonidae and generalists decreases. This may suggest that the parasitoids either respond negatively to temperature increases or that there are other more important factors at play. Whether they are directly or indirectly affected by temperature is not clear. See Hance et al. (2007) and Dyer et al. (2013) including sources within these for some information on how parasitoids may be affected by temperature. Both temperature and precipitation increased in period 3, and precipitation seems to lead to an increase in saproxylic Ichneumonoidea and generalists.

Adult Ichneumonoidea often drink water and may be dependent on moisture from morning dew (Hilszczański, 2018; Quicke, 2015; Townes, 1958). Shapiro and Pickering (2000) found that traps in wet forest caught 2.32 times more Ichneumonoidea than traps in moist forest, suggesting that rainfall is an important factor for the activity of these parasitoids. This study was conducted in tropical forests in Central America and had pseudoreplication in their design that made it difficult to conclude for certain if rainfall was the best explanation for the difference between their sites, or if other factors were more important (Shapiro & Pickering, 2000). Consequently, even though it provides valuable information, it is not directly comparable to my samples in temperate regions.

Precipitation could potentially create favorable conditions for the hosts of Ichneumonoidea (Quicke, 2015; Shapiro & Pickering, 2000), since at least some depend on moisture in dead wood; e.g., saproxylic Diptera (Ulyshen, 2018) and Coleoptera (Berkov, 2018; Gimmel & Ferro, 2018). A certain minimum amount of water is also required for the decay process to occur (Stokland et al., 2012), which in turn creates the habitat for the saproxylic insects (Stokland et al., 2012; Ulyshen & Šobotník, 2018).

Additionally, each subfamily may have different peaks in flight activity throughout the season, (Gaasch et al., 1998) which may explain the variation between the sampling periods. The variation at the species level may be too broad to know for certain which factor best

explain the observed increase in Ichneumonoidea between the periods. Even though the majority of Ichneumonoidea showed an increase in the third period in my results, it was not the case for saproxylic Ichneumonoidea and Euphorinae.
All this may be due to the factors discussed above in combination.

4.6 Sampling limitations

I was only able to categorize insects from one Malaise trap at each of the sites, and not two as originally intended. This, combined with only utilizing period 1 and 3, and not period 2 and 4, may have decreased the potential abundance of certain subfamilies due to the lack of spatial and temporal variation (Fraser et al., 2008). Malaise traps are often used to trap Ichneumonoidea, and particularly Ichneumonidae (Aguiar & Santos, 2010; Fraser et al., 2007, 2008; Mazón & Bordera, 2008; Quicke, 2015; Shapiro & Pickering, 2000). These traps collect 24/7 for 1-2 weeks between each bottle replacement, meaning that they are time and cost effective (Fraser et al., 2008; Quicke, 2015).

Certain trap characteristics could however potentially result in varying subfamily abundances (Quicke, 2015; Tao et al., 2012). Tao et al. (2012) found that, at certain sites, trap colors like yellow and green catch a greater number of Ichneumonidae than black and white. Additionally, the subfamilies Poemeniinae, Rhyssinae, and Metopiinae were scarcely trapped compared to their known existence in the study sites (Tao et al., 2012). Despite this, the black traps did catch more in one of their sites, and their traps were flight intercept traps based upon the design of a Malaise trap (Tao et al., 2012), which makes it slightly different from the ones I used. Similarly to Tao et al. (2012), I found a small number of Poemeniinae, Rhyssinae, and Metopiinae in my traps (Appendix 4). This finding could be a coincidence, or it could indicate that certain subfamilies are less likely to be collected by traps of certain colors (Tao et al., 2012), or maybe by certain traps in general (Aguiar & Santos, 2010; Mazón & Bordera, 2008; Quicke, 2015). Poemeniinae and Rhyssinae are both saproxylic (Broad et al., 2018; Hilszczański, 2018; Quicke, 2015), meaning that if data on these subfamilies were lost, it could potentially have contributed to the lack of difference in saproxylic Ichneumonoidea between the forest management types.

Malaise traps combined with other trap types, or different placements of Malaise traps in relation to the ground or canopy, could potentially have led to a greater coverage of all the subfamilies (Aguiar & Santos, 2010; Fraser et al., 2008; Mazón & Bordera, 2008; Quicke, 2015). This may be a topic for future studies. It is important to note that several of the studies I based my predictions on did not use Malaise traps (Hilszczański et al., 2005; Komonen et al., 2000; Stenbacka, Hjältén, Hilszczański, Ball, et al., 2010), which may have contributed to some different results. The Malaise traps in my study cover a relatively extensive area when combining all the sites, and even though the number of traps and periods were reduced, they may still give useful information about the trends in the abundance of Ichneumonoidea between the different forest management types.

5. Conclusion

The abundance of Ichneumonoidea were similar in mature clear-cut forests and near-natural forests at the family level. This was also evident for specialists, generalists, and saproxylic Ichneumonoidea. At the subfamily level, there were greater variation, with Cryptinae and Ichneumoninae being more abundant in NN, and Orthocentrinae showing signs of being more abundant in CC. This highlights the importance of studying these parasitoid wasps at the lowest possible taxonomic level, effectively removing the variation at higher taxonomic levels. Ichneumonidae, Orthocentrinae, and generalists had an increase in their abundance with the increase of total volume of dead wood, but this was not the case for saproxylic Ichneumonoidea. It is possible that other dead wood variables in combination with total volume could have given a different result. Additionally, my categorization of the saproxylic individuals may have been too broad to show any clear patterns. This shows that there may be considerable variation inside each saproxylic subfamily.

There were certain subfamilies exclusive to each forest management type, but the degree of difference was not tested in my study. The suggestion by Hilszczański (2018), Hilszczański et al. (2005), and Stenbacka, Hjältén, Hilszczański, Ball, et al. (2010) that none of the forest management types had a complete subfamily assemblage may be relevant, but was not specifically tested due to my focus on abundance. The complexity in the observed variation in parasitoid wasp abundance between the forest management types makes it difficult to conclude which forest management practice yields the most abundant parasitoid community.

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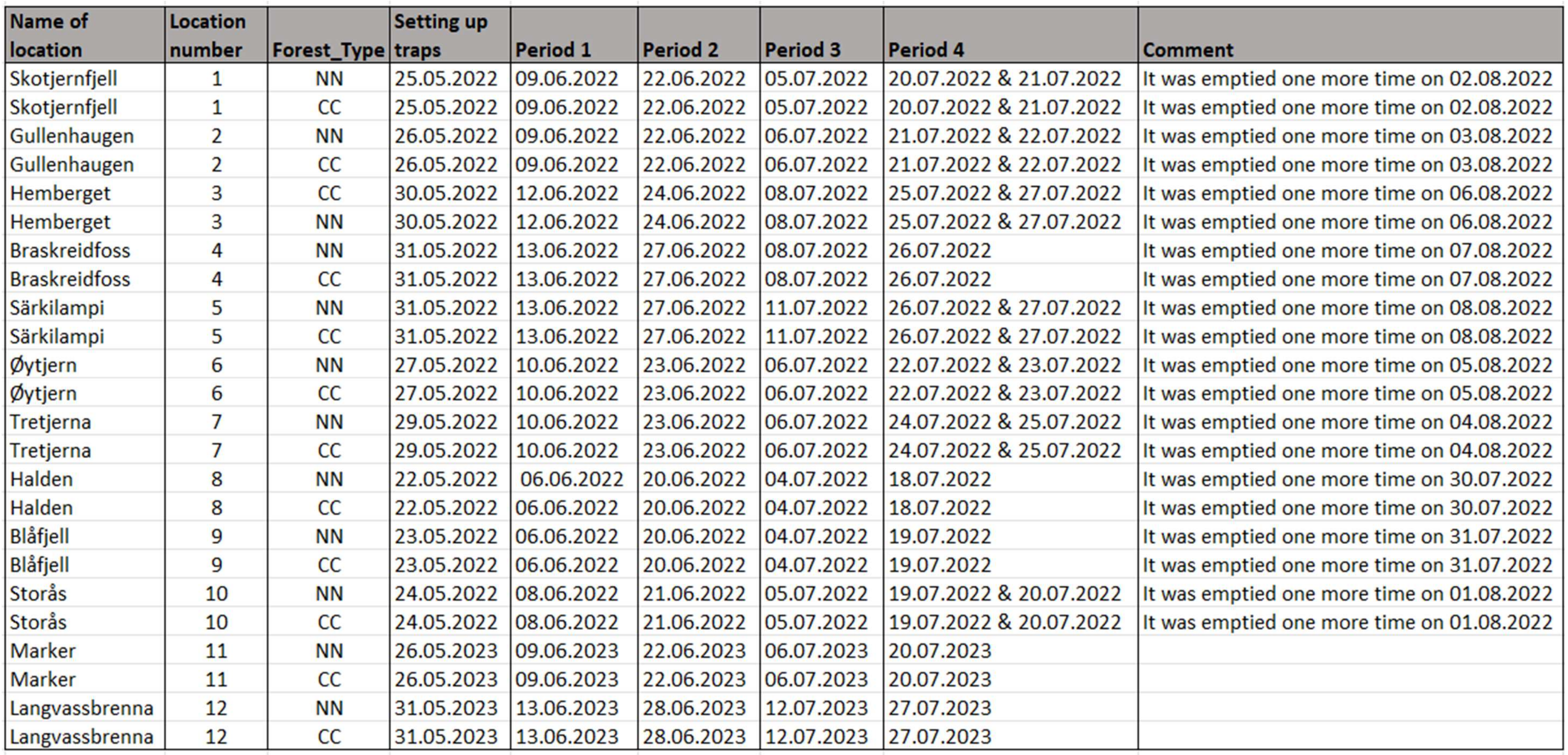
Appendix 1

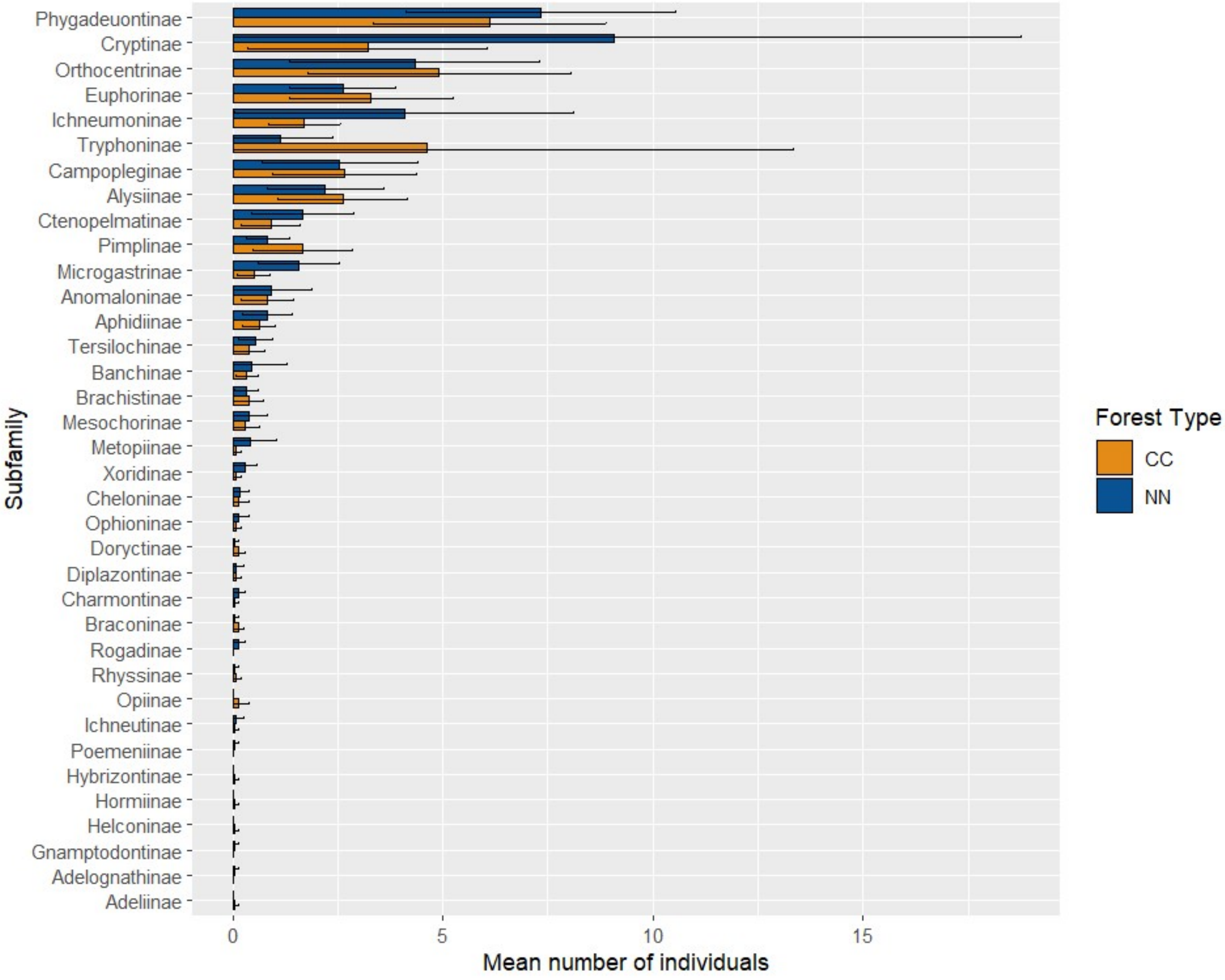
Overview of periods for emptying the traps.



Name of location	Location number	Forest_Type	Setting up traps	Period 1	Period 2	Period 3	Period 4	Comment
Skotjernfjell	1	NN	25.05.2022	09.06.2022	22.06.2022	05.07.2022	20.07.2022 & 21.07.2022	It was emptied one more time on 02.08.2022
Skotjernfjell	1	CC	25.05.2022	09.06.2022	22.06.2022	05.07.2022	20.07.2022 & 21.07.2022	It was emptied one more time on 02.08.2022
Gullenhaugen	2	NN	26.05.2022	09.06.2022	22.06.2022	06.07.2022	21.07.2022 & 22.07.2022	It was emptied one more time on 03.08.2022
Gullenhaugen	2	CC	26.05.2022	09.06.2022	22.06.2022	06.07.2022	21.07.2022 & 22.07.2022	It was emptied one more time on 03.08.2022
Hemberget	3	CC	30.05.2022	12.06.2022	24.06.2022	08.07.2022	25.07.2022 & 27.07.2022	It was emptied one more time on 06.08.2022
Hemberget	3	NN	30.05.2022	12.06.2022	24.06.2022	08.07.2022	25.07.2022 & 27.07.2022	It was emptied one more time on 06.08.2022
Braskreidfoss	4	NN	31.05.2022	13.06.2022	27.06.2022	08.07.2022	26.07.2022	It was emptied one more time on 07.08.2022
Braskreidfoss	4	CC	31.05.2022	13.06.2022	27.06.2022	08.07.2022	26.07.2022	It was emptied one more time on 07.08.2022
Särkilampi	5	NN	31.05.2022	13.06.2022	27.06.2022	11.07.2022	26.07.2022 & 27.07.2022	It was emptied one more time on 08.08.2022
Särkilampi	5	CC	31.05.2022	13.06.2022	27.06.2022	11.07.2022	26.07.2022 & 27.07.2022	It was emptied one more time on 08.08.2022
Øytjern	6	NN	27.05.2022	10.06.2022	23.06.2022	06.07.2022	22.07.2022 & 23.07.2022	It was emptied one more time on 05.08.2022
Øytjern	6	CC	27.05.2022	10.06.2022	23.06.2022	06.07.2022	22.07.2022 & 23.07.2022	It was emptied one more time on 05.08.2022
Tretjerna	7	NN	29.05.2022	10.06.2022	23.06.2022	06.07.2022	24.07.2022 & 25.07.2022	It was emptied one more time on 04.08.2022
Tretjerna	7	CC	29.05.2022	10.06.2022	23.06.2022	06.07.2022	24.07.2022 & 25.07.2022	It was emptied one more time on 04.08.2022
Halden	8	NN	22.05.2022	06.06.2022	20.06.2022	04.07.2022	18.07.2022	It was emptied one more time on 30.07.2022
Halden	8	CC	22.05.2022	06.06.2022	20.06.2022	04.07.2022	18.07.2022	It was emptied one more time on 30.07.2022
Blåfjell	9	NN	23.05.2022	06.06.2022	20.06.2022	04.07.2022	19.07.2022	It was emptied one more time on 31.07.2022
Blåfjell	9	CC	23.05.2022	06.06.2022	20.06.2022	04.07.2022	19.07.2022	It was emptied one more time on 31.07.2022
Storås	10	NN	24.05.2022	08.06.2022	21.06.2022	05.07.2022	19.07.2022 & 20.07.2022	It was emptied one more time on 01.08.2022
Storås	10	CC	24.05.2022	08.06.2022	21.06.2022	05.07.2022	19.07.2022 & 20.07.2022	It was emptied one more time on 01.08.2022
Marker	11	NN	26.05.2023	09.06.2023	22.06.2023	06.07.2023	20.07.2023	
Marker	11	CC	26.05.2023	09.06.2023	22.06.2023	06.07.2023	20.07.2023	
Langvassbrenna	12	NN	31.05.2023	13.06.2023	28.06.2023	12.07.2023	27.07.2023	
Langvassbrenna	12	CC	31.05.2023	13.06.2023	28.06.2023	12.07.2023	27.07.2023	

Appendix 2

Mean number of individuals in each subfamily between the forest management types sorted in descending order. Error bars indicate the 95% confidence interval around the mean (+2 SE (Standard error). (CC= former clear cut, NN= near natural).



Appendix 3

Overview of the tribes, genera, and species identified. This represent individual wasps that were possible to identify further than subfamily in the timeframe that was given to Alf Tore Mjøs and Jarl Birkeland.

Location	**Period**	**Forest management type**	**Subfamilies identified to tribe, genera and species.**
Skotjernfjell	1	NN	- One Anomaloninae, Tribe: Gravenhorstiini. - Three Phygadeuontinae, Genus: *Gelis*.
Skotjernfjell	1	CC	- Two Phygadeuontinae, Genus: *Gelis*. - One Ichneumoninae, Tribe: Phaeogenini. - One Hormiinae, Tribe: Hormiini, Genus: *Hormius*. - 11 Euphorinae in Genus: *Leiophron*, and one in Genus: *Elasmosoma*. - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - Two Anomaloninae, Tribe: Gravenhorstiini.
Gullenhaugen	1	NN	- One Anomaloninae, Tribe: Gravenhorstiini. - One Banchinae, Tribe: Atrophini, Genus: *Lissonota*. - One Orthocentrinae, Genus: *Orthocentrus*. - Two Phygadeuontinae, Genus: *Gelis*. - One Euphorinae, Genus: *Leiophron*, Species: *Leiophron pallidistigma* (Curtis).
Gullenhaugen	1	CC	- Two Ichneumoninae, Tribe: Phaeogenini. - One Orthocentrinae, Genus: *Orthocentrus*. - One Euphorinae, Genus: *Leiophron*, Species: *Leiophron pallidistigma* (Curtis).
Hemberget	1	NN	- One Anomaloninae, Tribe: Gravenhorstiini. - One Euphorinae, Genus: *Peristenus*.
Hemberget	1	CC	- One Phygadeuontinae, Genus: *Gelis*.

Braskereidfoss	1	NN	- One Ichneumoninae, Tribe: Phaeogenini.
Braskereidfoss	1	CC	- One Ichneumoninae, Tribe: Phaeogenini. - Two Phygadeuontinae, Genus: *Gelis*.
Särkilampi	1	NN	- One Ichneumoninae, Tribe: Phaeogenini. - One Euphorinae, Genus: *Leiophron*, Species: *Leiophron pallidistigma* (Curtis).
Särkilampi	1	CC	- One Phygadeuontinae, Genus: *Gelis*. - One Euphorinae, Tribe: Meteorini, Genus: *Zele*, Species: *Zele deceptor* (Wesmael). - One Ichneumoninae, Tribe: Phaeogenini.
Øytjern	1	NN	- One Xoridinae, Genus: *Xorides*. - One Ichneumoninae, Tribe: Phaeogenini. - One Phygadeuontinae, Genus: *Gelis*.
Øytjern	1	CC	- Two Anomaloninae, Tribe: Gravenhorstiini. - One Ichneumoninae, Tribe: Platylabini. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Aoplus*.
Tretjerna	1	NN	- One Phygadeuontinae, Genus: *Gelis*. - Three Ichneumoninae, Tribe: Phaeogenini. - Two Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - Two Orthocentrinae, Genus: *Orthocentrus*.
Tretjerna	1	CC	- Two Phygadeuontinae, Genus: *Gelis*. - Two Ichneumoninae, Tribe: Phaeogenini.
Halden	1	NN	- One Phygadeuontinae, Genus: *Gelis*. - One Orthocentrinae, Genus: *Orthocentrus*.
Halden	1	CC	- One Anomaloninae, Tribe: Gravenhorstiini.
Blåfjell	1	NN	- One Ichneumoninae, Tribe: Phaeogenini. - Two Rogadinae, Genus: *Aleiodes*. - 14 Euphorinae with two genuses: *Peristenus* and *Leiophron*.
Blåfjell	1	CC	- One Ichneumoninae, Tribe: Heresiarchini, Genus: *Coelichneumon*.

			- One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - One Banchinae, Tribe: Glyptini. - Three Orthocentrinae, Genus: *Picrostigeus*. - Two Phygadeuontinae, Genus: *Gelis*.
Storås	1	NN	- One Rogadinae, Genus: *Aleiodes*.
Storås	1	CC	- Six Euphorinae, Genus *Leiophron*.
Marker	1	NN	- One Ichneumoninae: Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Ichneumoninae: Tribe: Platylabini, Genus: *Platylabus*. - Two Phygadeuontinae, Genus: *Gelis*. - One Euphorinae, Genus *Leiophron*.
Marker	1	CC	- One Phygadeuontinae, Genus: *Gelis*. - Three Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - One Ichneumoninae, Tribe: Ichneumonini. - One Orthocentrinae, Genus: *Symplecis*.
Langvassbrenna	1	NN	- 17 Phygadeuontinae, Genus: *Gelis*.
Langvassbrenna	1	CC	- One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - Two Phygadeuontinae, Genus: *Gelis*. - One Ichneumoninae, Tribe: Phaeogenini. - 13 Euphorinae, Genus: *Leiophron*.
Skotjernfjell	3	NN	- Three Ophioninae, Genus: *Ophion*. - 11 Anomaloninae, Tribe: Gravenhorstiini. - 45 Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*. - Two Ichneumoninae, Tribe: Phaeogenini. - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla flavicoxis* (Thomson).

			- One Orthocentrinae, Genus: *Dialipsis*, Species: *Dialipsis exilis* (Förster). - One Xoridinae, Genus: *Odontocolon*, Species: *Odontocolon punctulatum* (Thomson). This is a new species for Norway. - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren).
Skotjernfjell	3	CC	- Three Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - One Pimplinae, Tribe: Pimplini, Genus: *Apechthis*, Species: *Apechthis quadridentata* (Thomson). - One Pimplinae, Tribe: Ephialtini, Genus: *Dolichomitus*, Species: *Dolichomitus terebrans* (Ratzeburg). - Two Ichneumoninae, Tribe Phaeogenini. - Seven Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - Two Anomaloninae, Tribe: Gravenhorstiini. - One Tryphoninae, Tribe: Tryphonini, Genus: *Polyblastus*, Subgenus: *Labroctonus*, Species: *Polyblastus (Labroctonus) westringi* (Holmgren). - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren).
Gullenhaugen	3	NN	- Three Ichneumoninae, Tribe: Phaeogenini. - Eight Ichneumoninae, Tribe: Ichneumonini, Genus: *Homotherus*, Species: *Homotherus varipes* (Gravenhorst). - Four Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - Four Anomaloninae, Tribe: Gravenhorstiini.

			- Three Pimplinae, Tribe: Pimplini, Genus: *Pimpla,* Species: *Pimpla flavicoxis* (Thomson). - Two Brachistinae, Tribe: Brachistini, Genus: *Eubazus.* - One Campopleginae, Genus: *Rhimphoctona,* Species: *Rhimphoctona xoridiformis* (Holmgren).
Gullenhaugen	3	CC	- One Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*. - Three Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Aoplus*. - Two Anomaloninae, Tribe: Gravenhorstiini. - Four Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla flavicoxis* (Thomson). - Four Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - Three Pimplinae: Tribe: Ephialtini, Genus: *Scambus*. - One Rhyssinae, Genus: *Rhyssa*, Species: *Rhyssa persuasoria* (Linnaeus). - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren). - One Xoridinae, Genus: *Odontocolon*. - One Braconinae, Genus: *Bracon*, Species: *Bracon pineti* (Thomson).
Hemberget	3	NN	- No information.
Hemberget	3	CC	- One Pimplinae, Tribe: Pimplini, Genus: *Pimpla,* Species: *Pimpla flavicoxis* (Thomson). - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Crypteffigies*, Species: *Crypteffigies lanius* (Gravenhorst). - One Tryphoninae, Tribe: Tryphonini, Genus: *Polyblastus*, Subgenus: *Polyblastus*, Species: *Polyblastus*

			(*Polyblastus*) *carbonator* (Kasparyan).
Braskereidfoss	3	NN	- One Ichneumoninae, Tribe: Heresiarchini, Genus: *Coelichneumon*, Species: *Coelichneumon cyaniventris* (Wesmael). - Two Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*.
Braskereidfoss	3	CC	- One Ichneumoninae, Tribe: Phaeogenini. - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren).
Särkilampi	3	NN	- Two Phygadeuontinae, Genus: *Gelis*. - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla flavicoxis* (Thomson). - One Ichneumoninae, Tribe: Heresiarchini, Genus: *Coelichneumon*, Species: *Coelichneumon cyaniventris* (Wesmael).
Särkilampi	3	CC	- One Euphorinae, Genus: *Centistes.* - One Orthocentrinae, Genus: *Orthocentrus*.
Øytjern	3	NN	- Three Ichneumoninae, Tribe: Ichneumonini, Genus: *Homotherus*, Species: *Homotherus varipes* (Gravenhorst). - One Anomaloninae, Tribe: Gravenhorstiini. - One Xoridinae, Genus: *Xorides*, Species: *Xorides alpestris* (Habermehl). - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren).
Øytjern	3	CC	- One Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*, Species: *Cratichneumon rufifrons* (Gravenhorst). - Two Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Aoplus*.

			- Six Anomaloninae, Tribe: Gravenhorstiini. - One Pimplinae, Tribe: Ephialtini, Genus: *Townesia*, Species: *Townesia tenuiventris* (Holmgren). - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona teredo* (Hartig). - One Brachistinae, Tribe: Brachistini, Genus: *Eubazus*.
Tretjerna	3	NN	- Four Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Ichneumoninae, Tribe Phaeogenini. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Chasmias*, Species: *Chasmias motatorius* (Fabricius). - One Adelognathinae, Genus: *Adelognathus*, Species: *Adelognathus stelfoxi* (Fitton, Gauld & Shaw). - One Pimplinae, Tribe: Ephialtini, Genus: *Dolichomitus*, Species: *Dolichomitus terebrans* (Ratzeburg). - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*. - One Pimplinae, Tribe: Ephialtini (or Polysphinctini or *Polysphincta* genus group), Genus: *Zatypota* (Artsdatabanken, n.d.-d; Broad et al., 2018; Gauld & Dubois, 2006; Gauld et al., 2002; Matsumoto, 2016; Wahl & Gauld, 1998). - One Brachistinae, Tribe: Brachistini, Genus: *Eubazus*. - Two Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren). - Three Xoridinae, Genus: *Odontocolon*, Species: *Odontocolon longitarsum* (Johansson). This is a new species for Norway.

Tretjerna	3	CC	- One Rhyssinae, Genus: *Rhyssa*, Species: *Rhyssa persuasoria* (Linnaeus). - Four Ichneumoninae, Tribe Phaeogenini. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*. - Four Anomaloninae, Tribe: Gravenhorstiini. - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - Three Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren). - One Xoridinae, Genus: *Odontocolon*, *Odontocolon dentipes* aggregate/species complex (Johansson, 2020, 2022). It is not certain which species it was inside this species complex. - One Helconinae, Tribe: Helconini, Genus: *Helcon*, Species: *Helcon tardator* (Nees).
Halden	3	NN	- Two Ichneumoninae, Tribe: Heresiarchini, Genus: *Coelichneumon*, Species: *Coelichneumon cyaniventris* (Wesmael). - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*. - 11 Tryphoninae, Tribe: Exenterini. - Two Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, one Species: *Pimpla turionellae* (Linnaeus) and one Species: *Pimpla flavicoxis* (Thomson). - One Cheloninae, Genus: *Ascogaster*, Species: *Ascogaster klugii* (Nees). - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona teredo* (Hartig).
Halden	3	CC	- One Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*. - One Ophioninae, Genus: *Ophion*. - One Tryphoninae, Tribe: Phytodietini, Genus: *Phytodietus*. - One Phygadeuontinae, Genus: *Gelis*.

			- One Campopleginae, Genus: *Rhimphoctona*.
Blåfjell	3	NN	- Two Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla flavicoxis* (Thomson). - One Pimplinae, Tribe: Ephialtini, Genus: *Clistopyga*, Species: *Clistopyga incitator* (Fabricius). - Four Ichneumoninae, Tribe: Phaeogenini. - Two Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - Two Charmontinae, Tribe: Charmontini, Genus: *Charmon*, Species: *Charmon cruentatus* (Haliday). - Two Cheloninae, Genus: *Ascogaster*, Species: *Ascogaster klugii* (Nees). - One Euphorinae, Genus: *Meteorus*. - Two Euphorinae, Genus: *Leiophron*. - One Poemeniinae, Genus: *Poemenia*, Species: *Poemenia brachyura* (Holmgren).
Blåfjell	3	CC	- Three Cheloninae, Genus: *Ascogaster*, Species: *Ascogaster klugii* (Nees). - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren). - Two Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona teredo* (Hartig). - One Ichneumoninae, Tribe: Phaeogenini. - One Brachistinae, Genus: *Diospilus*.
Storås	3	NN	- One Rhyssinae, Genus: *Rhyssa*, Species: *Rhyssa persuasoria* (Linnaeus). - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Gnamptodontinae, Genus: *Gnamptodon*, Species: *Gnamptodon pumilio* (Nees). - One Xoridinae, Genus *Xorides*. - A note on one species, namely *Helcostizus restaurator* (Fabricius) in Genus: *Helcostizus*. It was placed

			as the subfamily Cryptinae in this thesis due being placed as that in a document I got from Alf Tore Mjøs. Additionally, the genus *Helcostizus* is placed under Cryptinae in Hilszczański (2018). However, I noticed too late for incorporating it into my results that according to Artsdatabanken it is in the subfamily Phygadeuontinae (Artsdatabanken, n.d.-b). - One Campopleginae, Genus: *Rhimphoctona*, Species: *Rhimphoctona xoridiformis* (Holmgren). - One Anomaloninae, Tribe: Gravenhorstiini, Genus: *Therion*, Species: *Therion circumflexum* (Linnaeus).
Storås	3	CC	- One Pimplinae, Tribe: Pimplini, Genus: *Apechthis*, Species: *Apechthis quadridentata* (Thomson). - One Pimplinae, Tribe: *Pimplini*. - One Anomaloninae, Tribe: Gravenhorstiini. - Two Ctenopelmatinae, Tribe: Mesoleiini, Genus: *Saotis*, Species: *Saotis nigriventris* (Thomson).
Marker	3	NN	- Three Campopleginae, Genus: *Rhimphoctona*. - One Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - One Pimplinae, Tribe: Ephialtini, Genus: *Dolichomitus*. - One Phygadeuontinae, Genus: *Gelis*. - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Cratichneumon*. - One Orthocentrinae, Genus: *Orthocentrus*. - One Euphorinae, Genus: *Meteorus*.
Marker	3	CC	- One Metopiinae, Genus: *Exochus*. - 105 Tryphoninae, Tribe: Exenterini. - One Orthocentrinae, Genus: *Helictes*, Species: *Helictes erythrostoma* (Gmelin). - One Ichneumoninae, Tribe: Ichneumonini, Genus: *Ichneumon*.

			- One Ichneumoninae, Tribe: Ichneumonini, Genus: *Homotherus*, Species: *Homotherus locutor* (Thunberg). - One Banchinae, Tribe: Atrophini, Genus: *Lissonota*. - Four Phygadeuontinae, Genus: *Gelis*. - One Hybrizontinae, Genus: *Hybrizon*. - Two Pimplinae, Tribe: Pimplini, Genus: *Pimpla*, Species: *Pimpla turionellae* (Linnaeus). - Four Pimplinae, Tribe: Delomeristini, Genus: *Delomerista*, Species: *Delomerista pfankuchi* (Brauns). - One Pimplinae, Tribe: Ephialtini, Genus: *Dolichomitus*.
Langvassbrenna	3	NN	- Eight Phygadeuontinae, Genus: *Gelis*. - One Orthocentrinae, Genus: *Symplecis*. - Two Ichneumoninae, Tribe: Phaeogenini. - Two Anomaloninae, Tribe: Gravenhorstiini. - Three Euphorinae, Genus: *Meteorus*.
Langvassbrenna	3	CC	- Two Campopleginae, Genus: *Rhimphoctona*. - Three Phygadeuontinae, Genus: *Atractodes*. - Six Phygadeuontinae, Genus: *Gelis*. - One Phygadeuontinae, Genus: *Bathythrix*. - One Cryptinae, Tribe: Aptesini, Genus: *Javra*, Species: *Javra opaca* (Thomson). - One Pimplinae, Tribe: Ephialtini (Polysphinctini or *Polysphincta* genus group), Genus: *Sinarachna* (Artsdatabanken, n.d.-c; Broad et al., 2018; Gauld & Dubois, 2006; Gauld et al., 2002; Korenko et al., 2022; Matsumoto, 2016; Wahl & Gauld, 1998). - One Alysiinae, Tribe: Alysiini, Genus: *Heterolexis*. - Two Brachistinae, Genus: *Dyscoletes*, Species: *Dyscoletes lancifer* (Haliday).

Appendix 4

Total abundance of all Ichneumonidae and Braconidae subfamilies in both forest management types combined. "Specialist" (=koinobiont), "Generalist" (=idiobiont). If "Specialist" and "Generalist" are not present (not marked with "X"), it means the subfamily can be both specialist and generalist. If "Saproxylic" is not present, it means the subfamily is not saproxylic. There were 27 individuals across three subfamilies that could not be determined to generalist or specialist due to unknown life-history.

Subfamily	**Specialist**	**Generalist**	**Saproxylic**	**Abundance**	**Sources**
Adeliinae	X			1	Shaw and Huddleston (1991). This subfamily seems to have been moved to the subfamily Cheloninae in more recent papers even though it still stands as a subfamily at Artsdatabanken (Artsdatabanken, n.d.-a). Sources for being in Cheloninae: Chen and van Achterberg (2019); Jasso-Martínez et al. (2022); Kittel et al. (2016); Quicke (2015)
Adelognathinae				1	Broad et al. (2018); Quicke (2015)
Alysiinae	X			116	Chen and van Achterberg (2019); Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991)
Anomaloninae	X			42	Broad et al. (2018); Quicke (2015)

Aphidiinae	X			35	Chen and van Achterberg (2019); Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991)
Banchinae	X			19	Broad et al. (2018); Quicke (2015)
Brachistinae	X		X	17	Aubrook (1939); Chen and van Achterberg (2019); Hilszczański (2018); Jasso-Martínez et al. (2022); Kenis and Mills (1998); Sharanowski et al. (2011); Shaw and Huddleston (1991)
Braconinae		X	X	4	Chen and van Achterberg (2019); Hilszczański (2018); Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991)
Campopleginae	X		X	125	Broad et al. (2018); Hilszczański (2018); Luo and Sheng (2010); Quicke (2015)
Charmontinae	X			4	Chen and van Achterberg (2019); Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991)
Cheloninae	X			7	Chen and van Achterberg

					(2019); Jasso-Martínez et al. (2022); Kittel et al. (2016); Quicke (2015); Shaw and Huddleston (1991)
Cryptinae		X	X	295	Broad et al. (2018); Hilszczański (2018); Quicke (2015)
Ctenopelmatinae	X			62	Broad et al. (2018); Kasparyan and Kopelke (2010); Quicke (2015)
Diplazontinae	X			4	Broad et al. (2018); Quicke (2015); Wahl (1990)
Doryctinae		X	X	4	Chen and van Achterberg (2019); Hilszczański (2018); Jasso-Martínez et al. (2022); Jonsell et al. (2023); Quicke (2015); Shaw and Huddleston (1991)
Euphorinae	X		X	142	Ammunét et al. (2009); Chen and van Achterberg (2019); Hilszczański (2018); Huddleston (1980); Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991); Shaw (2004); Stigenberg and Hansen (2013)

Gnamptodontinae	X (?)			1	Belshaw et al. (2003); Quicke (2015); Shaw and Huddleston (1991) notes that it may be koinobiont, but what I realized too late for my results is that according to Chen and van Achterberg (2019) and Jasso-Martínez et al. (2022) it may be idiobiont.
Helconinae	X		X	1	Chen and van Achterberg (2019); Hilszczański (2018); Jasso-Martínez et al. (2022); Kenis and Hilszczanski (2004); Quicke (2015); Sharanowski et al. (2011); Shaw and Huddleston (1991)
Hormiinae		X		1	Jasso-Martínez et al. (2022); Jasso-Martínez et al. (2021); Quicke (2015); Shaw and Huddleston (1991)
Hybrizontinae	X			1	Broad et al. (2018); Quicke (2015)
Ichneumoninae				139	Broad et al. (2018); Godfray (1994); Hinz and Horstmann (2007); Perkins (1960); Quicke

					(2015); Shaw et al. (2015)
Ichneutinae	X			3	Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991)
Mesochorinae	X			16	Broad et al. (2018); Quicke (2015)
Metopiinae	X			12	Broad et al. (2018); Quicke (2015)
Microgastrinae	X			50	Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991); Whitfield et al. (2018)
Ophioninae	X			5	Broad et al. (2018); Quicke (2015)
Opiinae	X			3	Chen and van Achterberg (2019); Jasso-Martínez et al. (2022); Quicke (2015); Shaw and Huddleston (1991)
Orthocentrinae	X			222	Broad et al. (2018); Kolarov and Bechev (1995); Komonen et al. (2000); Quicke (2015); Roman (1939); Šedivý and Ševčík (2003); Shaw and Askew (2010); Short (1978); Vilkamaa and Komonen (2001); Wahl (1990); Wahl

					(1986, 1996); Waterston (1929)
Phygadeuontinae		X		323	Broad et al. (2018); Santos (2017); Schwarz and Shaw (1999, 2010)
Pimplinae			X	60	Broad et al. (2018); Eberhard (2000); Fitton et al. (1988); Gauld and Dubois (2006); Gauld et al. (2002); Hilszczański (2018); Korenko et al. (2022); Matsumoto (2016); Quicke (2015); Quicke et al. (2009); Shaw (2006); Wahl and Gauld (1998); (Weng & Barrantes, 2007)
Poemeniinae		X	X	1	Broad et al. (2018); Fitton et al. (1988); Gauld et al. (2002); Hilszczański (2018); Quicke (2015); Quicke et al. (2009); Shaw (2006); Wahl and Gauld (1998)
Rhyssinae		X	X	3	Broad et al. (2018); Chrystal and Skinner (1931); Fitton et al. (1988); Gauld et al. (2002); Hanson (1939); Hilszczański (2018); Madden (1968); Quicke (2015); Quicke et al. (2009); Shaw (2006);

					Spradbery (1970a, 1970b); Wahl and Gauld (1998)
Rogadinae	X			3	Jasso-Martínez et al. (2022); Jasso-Martínez et al. (2021); Quicke (2015); Shaw and Huddleston (1991)
Tersilochinae	X			22	Broad et al. (2018); Quicke (2015); Quicke et al. (2009)
Tryphoninae	X			138	Broad et al. (2018); Quicke (2015)
Xoridinae		X	X	9	Broad et al. (2018); Chrystal and Skinner (1931); Gauld and Fitton (1981); Hilszczański (2018); Johansson (2020, 2022); Quicke (2015); Spradbery (1970a, 1970b)

Appendix 5

Generalized linear mixed model of the abundance of Ichneumonidae (Model 3). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	1.426 (4.160)	0.259	5.503	**<0.001**
Period (3)	2.175 (8.806)	0.203	10.742	**<0.001**
Year (2023)	0.766 (2.150)	0.488	1.569	0.117
Forest type (NN)	0.152 (1.164)	0.205	0.743	0.457

Appendix 6

Generalized linear mixed model of the abundance of Orthocentrinae (Model 3). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	-0.579 (0.560)	0.404	-1.434	0.152
Period (3)	2.630 (13.870)	0.361	7.285	**<0.001**
Year (2023)	0.201 (1.223)	0.573	0.352	0.725
Forest type (NN)	-0.172 (0.842)	0.316	-0.543	0.587

Appendix 7

Optimal generalized linear mixed model of the abundance of Cryptinae (Model 2). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	-2.066 (0.127)	0.792	-2.608	**0.009**
Period (3)	3.049 (21.103)	1.160	2.629	**0.009**
Year (2023)	2.510 (12.300)	0.895	2.805	**0.005**
Forest type (NN)	1.167 (3.214)	0.520	2.246	**0.025**
Mean temperature	-0.444 (14.902)	0.512	-0.868	0.385
Mean precipitation	0.760 (8.815)	0.347	2.190	**0.029**
The random effect Site_ID has an estimated variance at zero.				

Appendix 8

Optimal generalized linear mixed model of the abundance of Ichneumoninae (Model 2). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	-1.267 (0.282)	0.547	-2.315	**0.021**
Period (3)	2.098 (8.152)	0.800	2.622	**0.009**
Year (2023)	0.819 (2.268)	0.763	1.073	0.283
Forest type (NN)	0.563 (1.755)	0.260	2.165	**0.030**
Mean temperature	-0.820 (14.062)	0.340	-2.413	**0.016**
Mean precipitation	0.677 (8.426)	0.265	2.560	**0.010**

Appendix 9

Optimal generalized linear mixed model of the abundance of Tryphoninae (Model 2). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	-7.354 (0.001)	2.145	-3.428	**<0.001**
Period (3)	9.255 (10454.630)	3.021	3.064	**0.002**
Year (2023)	3.971 (53.032)	2.087	1.902	0.057
Forest type (NN)	0.295 (1.344)	0.917	0.322	0.747
Mean temperature	-2.570 (12.540)	1.150	-2.235	**0.025**
Mean precipitation	-0.321 (5.582)	0.938	-0.342	0.732

The random effect Site_ID has an estimated variance close to zero ($5.881e^{-11}$).

Appendix 10

Model 1 Phygadeuontinae

Optimal generalized linear mixed model of the abundance of Phygadeuontinae (Model 1). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	0.794 (2.212)	0.343	2.313	**0.021**
Period (3)	1.691 (5.423)	0.559	3.023	**0.003**
Year (2023)	0.730 (2.074)	0.419	1.739	0.082
Forest type (NN)	-0.437 (0.646)	0.269	-1.626	0.104
Dead wood volume	0.280 (96.277)	0.145	1.925	0.054
Mean temperature	-0.188 (15.683)	0.260	-0.725	0.468
Mean precipitation	0.024 (6.265)	0.175	0.135	0.892
Connectivity	0.303 (575088.552)	0.151	2.005	**0.045**

Model 3 Phygadeuontinae

Generalized linear mixed model of the abundance of Phygadeuontinae (Model 3). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	0.670 (1.954)	0.284	2.360	**0.018**
Period (3)	1.330	0.217	6.121	**<0.001**

	(3.781)			
Year (2023)	0.527 (1.694)	0.520	1.015	0.310
Forest type (NN)	0.160 (1.173)	0.212	0.754	0.451

Appendix 11

Optimal generalized linear mixed model of the abundance of Euphorinae (Null model). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	1.085 (2.958)	0.199	5.439	**<0.001**

The random effect Site_ID has an estimated variance at zero.

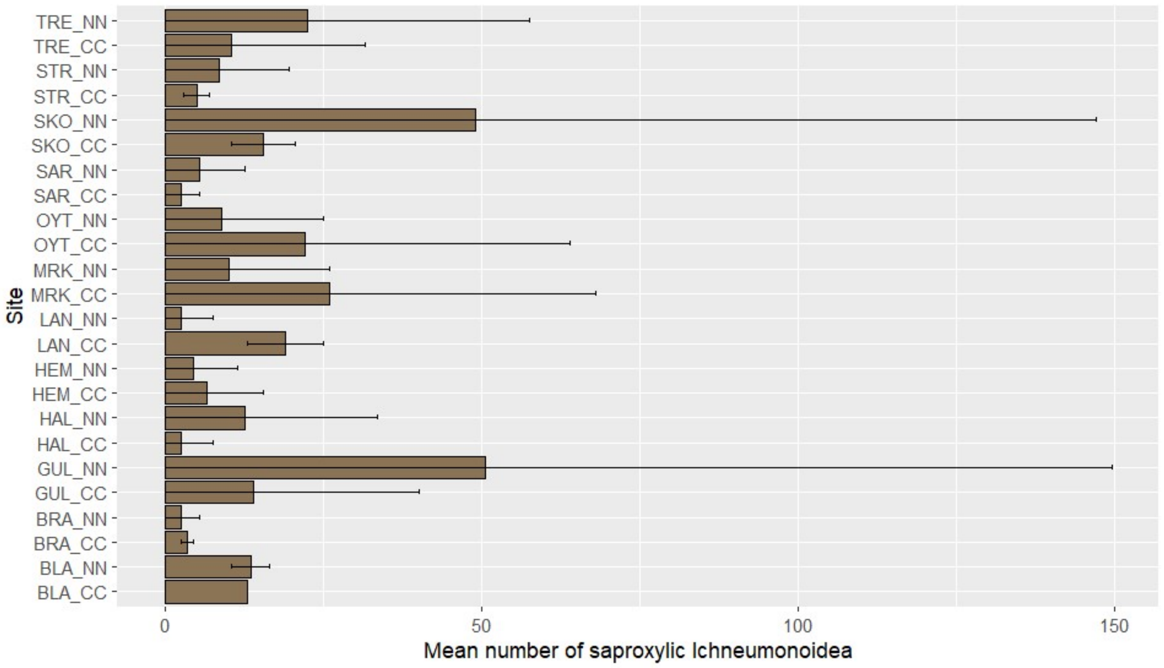
Appendix 12

Generalized linear mixed model of the abundance of generalists (Model 3). Site ID is included as a random effect. The estimates are expected log counts with backtransformed values in parenthesis. p-values <0.05 are in bold.

Fixed effect	Estimate	SE	z-value	p-value
Intercept	1.141 (3.131)	0.297	3.838	**<0.001**
Period (3)	1.691 (5.425)	0.230	7.341	**<0.001**
Year (2023)	0.572 (1.771)	0.569	1.006	0.315
Forest type (NN)	0.240 (1.271)	0.227	1.057	0.291

Appendix 13

Mean number of saproxylic Ichneumonoidea across the different sites. Error bars indicate the 95% confidence interval around the mean (+2 SE (Standard error)). (CC= former clear cut, NN= near natural).



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