

Norwegian University of Life Sciences

Master's Thesis 202460 ECTSFaculty of Environmental Sciences and Natural Resource Management

Long-term influence of forest management on Diptera abundance

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Preface

This year has been a rough one, but I have endured and managed to land the assignment with some extra time over the summer. Without the compassion and understanding from my two lovely supervisors, Lisa Fagerli Lunde and Tone Birkemoe, this would not have been possible. Thanks for the comfort and stress-guidance, and for the brutal honesty when my mind have been all over the place. Also, thanks Lisa, for recommending the ForBio Diptera course at the Faroese Islands. The experience was amazing, and I even made a discovery of the Diptera family, Heterocheilidae, previously undocumented in the Faroese Islands (left picture showing *Heterocheila buccata*). The knowledge I gained at the course was priceless for the sorting process on the lab.

A big thanks to Tone Granerud for lending me a stereo microscope over the holidays, and all the good conversations and guidance on the lab. Thanks to Milda Norkute for insight on DNA metabarcoding, and for all the funny conversations. Thanks to Johan Asplund for helping me out with the weather variables. In addition I have to mention one of the most polite and kind monkeys I have ever met, Brian Moe Holter. Thank you for the superb company during our fieldwork, on the lab, and for all the help you provided. Without your assistance this thesis would have been much more challenging than it already was, so I owe you big time!

To Elisabeth <3. You pushed me into pursuing this education, and without you I would still be a confused, art school failure, trying to navigate the world without a map and compass. Thanks for putting up with me for all these years. Last, a big thanks to Alfred for always cheering me up (right picture). Du och jag, Alfred!



Øystein Bakke August 14th, 2024

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Abstract

Intensive forestry practices, particularly clear-cutting, have significantly altered Norway's forest landscapes since the mid-20th century. This shift away from traditional, more selective logging methods, has in many areas reduced the forest habitat connectivity and dead wood availability, which are known to be important for many insects. To understand the consequences from these forestry practices, it is essential to perform comparability studies between forest types.

In this study, Diptera were sampled using Malaise traps across 12 forest pairs in southeastern Norway to compare Diptera abundance between two forest types. Each pair consisted of one mature clear-cut stand and one near-natural forest stand. The samples were sorted, counted, and identified to the family level. They were also analysed both at the individual family level and collectively as total Diptera and saproxylic Diptera. Other potential predictor variables, such as dead wood volume, connectivity, period and weather variables were also measured. The results were analysed using a general linear mixed model (GLMM).

The results revealed few differences in abundance between mature clear-cuts and near-natural forests, except for Phoridae, who were more abundant in mature clear-cuts. Dead wood was correlated only with the abundance of Tipulidae, while connectivity showed a correlation with saproxylic families as a group, as well as with some selected families.

To better understand the correlation between forest types and Diptera abundance, the study design could be improved using other trap types and an extended sampling period. Identifying Diptera to the species level is necessary, as broad ecological variation within many Diptera families can mask potential effects of forest type. Advances in DNA metabarcoding may offer a promising approach to overcome challenges in Diptera species identification.

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1. Introduction

Insects are an essential part of forest biodiversity and play fundamental roles in forest ecosystems (Courtney et al., 2017; Frouz, 1999; Pape, 2009; Ulyshen et al., 2018). Their diverse functions include services such as, pollination, pest control, decomposition, aeration of the soil and nutrient cycling (Courtney et al., 2017; Frouz, 1999). One of the most ecologically diverse orders of insect are the Diptera (Courtney et al., 2017; Pape, 2009; Ulyshen, 2018), known as midges, gnats, mosquitoes and flies. As highly abundant insects in the northern hemisphere, many species of Diptera also operates as a vital food source for many vertebrates (Courtney et al., 2017). They are also considered valuable pollinators in alpine and arctic environments, and are often specialised on certain plants (Courtney et al., 2017; Griffiths, 1997).

Today, insects are experiencing a concerning global decline (Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021). This trend is partly driven by human actions such as habitat alteration, unsustainable land-use practices, and deforestation (Hallmann et al., 2017; Seibold et al., 2019; Wagner et al., 2021). In Norway, only 1,6 % of the productive forest can be termed natural (Framstad et al., 2021). This low figure is of particular concern as many as 84% of the red listed species found in forests depend on forests older than 180 years (Artsdatabanken, 2021a). Many species thriving in natural forests are specialists reliant on rare microhabitats (Nordén et al., 2013). For instance, several species of Mycetophilidae (fungus gnats) are known to utilise fungi associated with dead wood, and thrive in areas of high connectivity, characterised by dead wood and tree age variation (Økland, 1994).

The forests in Norway have long been influenced by humans, with forestry practices significantly shaping the forest structure (Esseen et al., 1997; Kuuluvainen et al., 2012; Storaunet et al., 2005). Historically, small-scale disturbance events in the forests such as single-tree falls or insect outbreaks, created gaps in the forest canopy (Kuuluvainen & Aakala, 2011; McCarthy, 2001). These events initiated ecological succession and created a complexity in the forest structure, that contributed to biodiversity and ecosystem resilience (McCarthy, 2001).

Up until the mid-20th century, different types of selective cuttings were the primary method used for logging (Kuuluvainen et al., 2012). This approach involved logging individual or small groups of trees. Thus, even though large timber volumes were removed, they maintained a diverse forest structure (Lie et al., 2012). By the 1950s, a shift occurred in

Fennoscandian forestry practices, as stand replacing clear-cutting became the dominant logging method (Bartlett et al., 2020; Kuuluvainen et al., 2012; Storaunet et al., 2005; Östlund et al., 1997).

Clear-cutting removes all trees within a designated area and typically involves replanting with a single, fast-growing species, such as *Picea abies* (Norway spruce). The forest patch is normally thinned twice until they are harvested between 60 and 120 years old. This approach significantly shortens the rotation period compared to the tree's natural lifespan (Bartlett et al., 2020; Kuuluvainen et al., 2012; Stokland et al., 2012) which can be up to 450 to 470 years for *P. abies* (Esseen et al., 1997). Consequently, this prevents gap dynamics to occur (Kuuluvainen, 2009), which impacts the forest in many ways. The accumulation of dead wood of greater proportions are reduced (Kuuluvainen, 2009; Kuuluvainen et al., 2012; Stokland et al., 2009; Kuuluvainen et al., 2012; Stokland et al., 2009; Kuuluvainen et al., 2012; Mich et al., 2012), alongside with the heterogeneity of the forest structure (Esseen et al., 1997; Nordén et al., 2013). This can be detrimental to many different organisms, especially those dependent on dead wood for survival or specific life stages. These saproxylic organisms are particularly vulnerable to the reduced quantities of dead wood and overall biodiversity decline (Siitonen, 2001).

In Norway, only 30% of the productive forests have never been clear-cut (Storaunet & Rolstad, 2020), emphasising the extensive impact of the stand replacement forestry.

Previously managed forests are gradually shifting to a state of natural regeneration, and form characteristics of old-growth forests, if left undisturbed. This includes structural complexity, characterised by a diversity of tree age and sizes, increased volume and types of dead wood, and multi-layered canopies. These near-natural forests can become valuable habitats over time, potentially matching biodiversity found in old-growth forests (Jacobsen et al., 2020; Ohlson et al., 1997; Stenbacka et al., 2010; Storaunet et al., 2005).

Currently, near-natural forests harbour a greater diversity of Coleoptera compared to mature clear-cuts, because of increased volumes of dead wood (Jacobsen et al., 2020). Dead wood serves as an essential resource, providing food, shelter, and breeding sites for approximately 20-30% of forest-dwelling insects in northern Europe (Birkemoe et al., 2018; Stokland et al., 2012; Ulyshen et al., 2018).

Diptera is a very ecological diverse order of insects which occupy many different habitats both on land and in water, and they are often the most abundant insects found in decaying wood (Ulyshen, 2018). They may also be the most diverse insect group utilising dead wood

in the Nordic region. However, our knowledge of this is limited due to the difficulty of identification (Stokland et al., 2012). In Norway there are approximately 5300 described species of Diptera, but estimations suggest there to be more than 10 000 species (Artsdatabanken, 2022). Worldwide, Diptera in general might make up for roughly 80-90% of all insects fostered from rotting wood (Hilt & Ammer, 1994). This shows that the ecological contributions from Diptera are fundamental to forest ecosystems (Pape, 2009). Many soil-dwelling Diptera play an important part in soil dynamics, where they break down organic litter and help with nutrient cycling (Courtney et al., 2017; Frouz, 1999; Pape, 2009). Even though the impact and importance of soil-dwelling Diptera for soil functioning is apparent, their fauna and ecology are less studied (Pape, 2009).

One of the most numerous Diptera related to dead wood is the Mycetophilidae (fungus gnats) (Siitonen, 2001). The mycetophilids have an affinity for old forest, as these are important habitats for a variety of different fungi (Økland, 1996). They are affiliated with both fungi growing on dead wood, and fungi in the soil (Økland, 1994), but relatively few species are found in non-fungal habitats (Økland, 1996). Mycetophilids have been shown to be sensitive to clear-cutting, as the practice disrupts the connectivity of the fungal structure in both the soil and above ground dead wood (Økland, 1994).

The diverse life histories of the many saproxylic dipterans are closely tied to specific dead wood habitats, reflecting the varied ecological niches created by different age classes and stages of decay (Ulyshen, 2018). Some of these habitats are created relatively fast, such as fallen branches with moist decaying wood (Rotheray et al., 2001), or sap exudation from wounded trees (Wolton & Luff, 2016). However, most other habitats concerning dead wood take years to form. Kelo trees are ones such limited form of dead wood. These are old, twisted, barkless pines shaped by centuries of weathering (Löfroth et al., 2023). The development of kelo trees and other slow-developed habitats, emphasises the importance of habitat connectivity for maintaining biodiversity. The loss of these important habitats could lead to the extinction of specialised species.

Estimates tell that Diptera might even surpass Coleoptera in species richness, but the research on this order of insect is rather insufficient (Ulyshen, 2018). While research on northern insect orders often favours Coleoptera, large-scale surveys can reveal important and surprising results. The Swedish Malaise Trap Project, encompassing 73 traps across Sweden from 2003 to 2009, revealed that Diptera and Hymenoptera far outnumbered Coleoptera and

other insect orders (Karlsson et al., 2020; Ronquist et al., 2020). This emphasises the potential ecological significance of Diptera and the gaps in our knowledge about them.

The main objective of this thesis is to examine whether forest management types, mature clear-cut and near-natural spruce forests, affect Diptera abundance. The quantity of dead wood and habitat connectivity varies considerably between the forest types, but also among the different sites within the study. Therefore, dead wood and connectivity will be analysed as continuous variables to examine their correlation with Diptera abundance. Other factors, such as collection period, precipitation, and temperature will also be evaluated as potential predictors.

The hypotheses will be tested on the following levels:

- 1. Total Diptera abundance all collected Diptera, excluding Sciaridae.
- 2. Saproxylic Diptera abundance all Diptera classified as saproxylic, excluding Sciaridae.
- **3.** Selected saproxylic families abundance Families \geq 30 individuals from all sites.

H1:Near-natural forests have a higher number of Diptera than clear-cut forests.

H2: Diptera abundance is correlated with dead wood.

H3: Diptera abundance is correlated with habitat connectivity.

2. Materials and methods

2.1 Study area, design and selection criteria

My thesis is part of the project EcoForest: "Forestry effects on biodiversity, carbon stock and ecological processes in mature boreal forests". The project is a collaboration between The Norwegian University of Life Sciences (NMBU), the University of Oslo (UiO), the Norwegian Institute of Bioeconomy Research (NIBIO) and Norwegian Institute for Nature Research (NINA). It is financed by the Norwegian Research Council (Ecoforest, 2021).

Twelve study sites were established in southeastern Norway (Fig. 2.1), each containing two mature boreal forest stands forming a "forest pair". One stand within each pair is a nearnatural (NN) forest, meaning they are developing characteristics of old forests, such as increasing dead wood volumes and diverse vegetation structures. These forests have not undergone clear-cutting, although some selective logging have occurred in the past. The other forest stand in the pair is a mature clear-cut (CC) approaching the typical harvest age of 70-80 years. The NN and CC represent two different forest managements but are referred to as forest type henceforward. Sites were chosen based on similar soil conditions (edaphic conditions), comparable canopy structures, matching productivity levels, southerly aspects, similar topography, and a distance of approximately 5 kilometres between each forest type within a pair. Furthermore, there were no signs of infestation from the European spruce bark beetle (*Ips typographus*), and the dominant tree species at all locations was *P. abies* (Asplund, 2024).

Maps and aerial photographs from the 1960s guided the selection of the sites. NN stands were initially chosen from nature reserves and then confirmed by continuous canopy cover visible in the aerial photographs. CC stands were identified by showing an absence of forest cover, with subsequent photographs indicating forest regrowth over time (Asplund, 2024).



Figure 2.1 The 12 sites in the EcoForest project. Source: EcoForest

2.2 Insect sampling

The insects collected from sites 1 - 10 were gathered between the end of May and start of August in 2022, by previous master students and staff at NMBU. Brian Moe Holter and I gathered our insect samples from site 11 & 12 (Marker and Langvassbrenna respectively) between May and start of August in 2023 (App. A, Table A.1)

Within each forest stand across all sites, a 15 x 15-meter main plot was nested within a larger 133.33 x 15 meter transect. Insect were collected with Malaise traps (BugDorm, Taiwan). Two Malaise traps were installed outside the northern and southern outskirts of the main plot,

in all sites (Fig. 2.2; Fig. 2.3). In the end, only insects from the northern Malaise trap samples were counted and identified due to time constraints.



Figure 2.2 Malaise trap set-up. Malaise traps were installed at all 12 study sites. Each site included a forest pair, consisting of one NN and one CC forest stand. Each forest stand comprised of a 15 x 15 m main plot (mid square) where temperatures (°C) were recorded by other EcoForest students and staff. Malaise traps were placed on the north and south outskirts of the main plot, within a greater transect (133.33 x 15 m) installed by past master students and staff, for dead wood surveys. Aluminium foil covered the north-side trap bottle to protect sample DNA from heat and UV radiation, as another project within Ecoforest required the DNA to be intact for metabarcoding. Illustration: Øystein Bakke



Figure 2.3 Left: Traps installation at the NN site at location 11. (Marker), the 26th of May 2023 (Photo: Brian Moe Holter). Right: Trap installation at the NN site at location 12. (Langvassbrenna), the 31st of May (Photo: Øystein Bakke). Malaise traps (BugDorm, Taiwan) in both pictures.

For stability, each trap was secured to a tree at one end. The traps were placed in relatively open areas, allowing insects easy access from all sides for flight entry. In collaboration with another EcoForest project studying insect DNA, the trapping bottle on all the north-facing Malaise traps was covered in aluminium foil. This was necessary to prevent degradation of the sample DNA by UV-radiation and high temperatures. Following each collection period, the samples were transported back to the university and stored in a -20°C freezer (Fig. 2.4).

During the first three collection periods, the traps contained 96% ethanol for sample preservation. However, due to a previous year's error, the traps for the fourth period were filled with 85% ethanol.



Figure 2.4 Left: Bottle on a north facing Malaise traps covered with aluminium foil. The bottle was marked "MAR CC 3 MN", which stands for Marker (the municipality), clear-cut (forest type), 3 (the period), MN (Malaise North). Middle: The bottle of the south facing trap without aluminium foil, marked the same way as the others. Right: Samples brought back to the university to be stored in a freezer at -20 °C.

Due to time constraints, only trap samples collected during the first and third sampling periods from north-facing Malaise traps were sorted and counted.

2.3 Predictor variables

Environmental data describing the study sites was available from the EcoForest project.

Volumes of Dead wood (standing and downed dead wood volumes $(m^3 ha^{-1})$ with a diameter of 5 cm or greater at breast hight or base) and decay classes (fresh to well-decomposed) were measured in transects (133.33 x 15 metres plot) (Asplund, 2024).

Connectivity was calculated by the sum of living spruce volume ($m^3 ha^{-1}$) exceeding 80 years located within a 25 km radius from each plot center. Calculations assumed an average dispersal distance of 0.5 km (i.e. alpha = 2) (Asplund, 2024).

Temperatures were recorded using TMS-4 dataloggers (TOMST s.r.o, Praha, Czech Republic), positioned at six points in the main plot. Temperatures were recorded 15 cm above the ground, every 15 minutes (Asplund, 2024). Temperature data was provided to us by Milda Norkute, and used to calculate mean temperature per site and for the relevant periods.

Precipitation data for 2022 and 2023 was obtained from the Norwegian Meteorological Institute (MET Norway) archives using each sites coordinates with seNorge2018_2022.nc and seNorge2018_2023.nc datasets (Lussana et al., 2018). Mean daily precipitation per site and period was calculated using Rstudio together with Brian Moe Holter.

2.4 Response variables

The analyse focused on the following response variables: total Diptera abundance, saproxylic Diptera abundance, Sciaridae (Black-winged fungus gnats), Phoridae (Scuttle flies), Mycetophilidae, Anthomyiidae (Root-maggot flies), Empididae (Dagger flies), Muscidae (House flies), Hybotidae (Dance flies), Chironomidae (Lake flies), Dolichopodidae (Longlegged flies), Syrphidae (Hoverflies), Tachinidae (Tachinid fly), Pipunculidae (Big-headed flies), Fanniidae (House flies), Tipulidae (Large crane flies), Limoniidae (Crane flies). Sciaridae was analysed separate from the total Diptera abundance and saproxylic Diptera abundance, due to overwhelming numbers compared to the other families.

All saproxylic families were identified based on their life history strategies and substrate preferences as described by Ulyshen (2018). Most families within the saproxylic group also had the ability to utilise substrates other than dead wood, classifying them as facultative saproxylics.

2.5 Laboratory processing - sorting and identification

As part of another branch of the EcoForest project led by Milda Norkute, samples from the north-facing Malaise traps were shipped to the University of Oslo (UiO), for DNA metabarcoding analysis. Brian Moe Holter and I assisted with the lab work. The samples were lysated (where the cell-membrane of the samples were broken down prior to DNA extraction) with lysation buffer (ATL) and proteinase K. Once the DNA metabarcoding was complete, the samples returned to the NMBU entomology lab for sorting.

Each sample was sifted through a fine-mesh sieve to separate the insects from the ethanol solution. Specimens were subsequently put into a petri dish with 85% ethanol and sorted using a stereo microscope (Olympus SZ51). The initial sorting stage, conducted in collaboration with Brian Moe Holter, involved classifying the specimens into three primary orders: Coleoptera, Hymenoptera, and Diptera. Specimens falling outside of these three orders were excluded from the initial count. Sorted specimens from each site were preserved in a 85% ethanol solution. Depending on sample size, they were stored in either 6 ml (22.5 ml) or 8 ml (30 ml) glass vials. Each vial was labelled with site ID, forest type, cardinal direction, trap ID and date.

I counted and identified all the Diptera specimens to family (Appendix A, Table A.2.), using Oosterbroek's (2006) "The European families of the Diptera".

The extent of the damage from the lysation process made identification of some of the most fragile insects very difficult. The family of Cecidomyiidae was particularly affected. Despite identifying some morphological features suggestive of their family, the majority of specimens were too incomplete or damaged for a decent family-level identification. Consequently, all Cecidomyiidae individuals were excluded from the analysis to ensure data integrity.

2.6 Statistical analysis

Data analysis was conducted following the guidelines of Zuur et al., (2010), Bolker et al., (2009), and Harrison et al., (2018). Statistical analyses and visualisation were made with R version 4.2.2 (R Core Team 2024) and Rstudio version 2023.12.0+369. Tables were visualised using Microsoft® Excel® for Microsoft 365 MSO (Version 2407 Build 16.0.17830.20056) 64-bit.

Given the right-skewed distribution of my count data, generalised linear mixed models (GLMMs) were used for the analysis. GLMMs are flexible, and can handle non-normal data without errors, while including both fixed and random effects. This makes GLMMs suitable for modelling complex ecological data (Bolker et al., 2009). Consequently, a Poisson distribution within the GLMM framework was chosen for further analysis (Bolker et al., 2009).

To account for possible variation among count data from the same sites that might not be explained by other factors in the model, "Site" (Site ID) was included as a random effect (Bolker et al., 2009; Harrison et al., 2018). To address overdispersion in my count data, I incorporated an observation-level random effect (OLRE) into the model, acknowledging that there might be some unexplained variability specific to each observation (Harrison et al., 2018). This involved creating a unique identifier ("Obs ID") for each row in the data set.

Within the GLMM framework, fixed effects represent the direct influence of a variable on the response variable. Random effects, on the other hand, capture the variation among experimental units, accounting for potential influences from these variations on the response variable. The positive expected value in a Poisson distribution requires the use of the log-link function for parameter estimation. Therefore, the model outputs are presented on the natural

logarithmic scale (Bolker et al., 2009). The "glmer" function from the "lme4" package (version 1.1-35.3) in Rstudio was used to fit the GLMMs (Bates et al., 2014).

To ensure comparability and address potential issues occurring from the scale difference between predictor variables (Appendix A, Table A.3), I standardised the numerical values so I could compare them on a common scale. This was done prior to model fitting. The mean (\overline{y}) was subtracted from each value (y_i) and then divided by the standard deviation of the variable (s_y) , resulting in a new variable called (z_i) , which now has a mean of 0 and a standard deviation of 1 (Eq. 2.1).

(Eq. 2.1)
$$Z_i = \frac{y_i - \overline{y}}{s_y}$$

This was done following the theoretical framework of Legendre & Legendre (2012), (page 44) and completed with the "scale" function in Rstudio.

To identify the most influential variables driving the observed patterns in Diptera abundance, pre-selected candidate models (a priori models) were employed, based on ecological relevance and the hypotheses (Harrison et al., 2018). These models included the predictor variables fitted to each response variable. Six alternative Poisson regression models for each response variable were explored, including one zero-model (Table 2.1.).

The saproxylic Diptera chosen for the candidate models included all saproxylic Diptera families with a total count of \geq 30 individuals. The threshold of 30 was selected as a practical limit to ensure sufficient sample size for statistical analysis.

The Akaike Information Criterion (AIC) was used to identify the model that best explains the observed patterns in the count data for each response variable. The AIC balances model fit with complexity, favouring models that accurately represent the data while using a minimal number of predictor variables. The model displaying the lowest AIC values is considered the most suitable (Bolker et al., 2009).

To check for collinearity among predictor variables I examined the Variance Inflation Factor (VIF) for all models. Multicollinearity happens when predictor variables in a model exhibit high correlations, meaning the lower VIF values the better (Harrison et al., 2018). The VIF results for all models were below 5, which is decent as anything under 10 is often considered acceptable (Curto & Pinto, 2011).

Table 2.1. Predictor variables used for the a priori candidate models. The analyse focused on the followingresponse variables: total Diptera abundance, saproxylic Diptera abundance, Sciaridae, Phoridae,Mycetophilidae, Anthomyiidae, Empididae, Muscidae, Hybotidae, Chironomidae, Dolichopodidae, Syrphidae,Tachinidae, Pipunculidae, Fanniidae, Tipulidae, Limoniidae. Sciaridae was analysed separate from the totalDiptera abundance and saproxylic Diptera abundance, due to overwhelming numbers compared to the otherfamilies.



* Random effects (site and observation-level random effect (OLRE))

When evaluating the correlation between responses and predictors, I also considered the "strength of the evidence" to identify potential trends, rather than relying only on statistical significance ($p \le 0.05$) (Muff et al., 2022) (App. A, Table A.4.).

For the following results, the predictor, "year", was only included due to the addition of two new sites in 2023. Even though year display a level of significance for some of the response variables, the predictor itself is not of substantial interest for the analysis and will not be discussed. Additionally, forest management will be referred to as "forest type" for the following results and discussion.

3. Results

A total of 31,442 individuals were sorted from the 24 malaise traps over two sample periods. The composition of the major insect orders exhibited a dominance of Diptera, with Hymenoptera as the second most abundant, and Coleoptera as the least abundant (Fig. 3.1). A total of 22,429 dipterans were identified to 45 families (App. B, Table B.1.), with Sciaridae being the most abundant family.



Figure 3.1 Comparison of the total composition of the three insect orders across both forest types, for all sites combined. The two left columns show the composition including the dipteran family Sciaridae. The two right columns show the composition excluding Sciaridae.

3.1 Total Diptera Abundance

Diptera abundance, without Sciaridae, did not differ significantly between the forest types (Fig 3.2; App. B, Table B.1). Although not significant, there was a weak evidence (p = 0.073) for a correlation between Diptera abundance and connectivity (App. B, Fig. B.1). The total abundance was higher in period 3 than period 1 (p < 0.001). Total dead wood volume, mean temperature and mean precipitation did not remain in the best model (App. B, Table B.2.).



Figure 3.2 Boxplot showing the abundance of Diptera (without Sciaridae) in near-natural and mature clear-cut forest, for period 1 and 3. Each data point is shown as a faded dot, which represent each northbound trap from the 12 sites in the project. Data points falling outside the whiskers are considered outliers and are depicted here as the solid black dots.

3.2 Saproxylic Diptera Abundance

There was no effect of forest type on the saproxylic Diptera (without Sciaridae) (Fig. 3.3), but there was strong evidence (p = 0.004) for an increase in abundance with connectivity (Fig. 3.4; App. B, Table B3). Saproxylic Diptera increased in abundance from period 1 to period 3 (p < 0.001). Neither dead wood, precipitation, or temperature were included in the optimal model (App. B, Table B4.).



Figure 3.3 Boxplot showing the abundance of saproxylic Diptera (without Sciaridae) in near-natural and mature clear-cut forest, for period 1 and 3. Each data point is shown as a faded dot, which represent each northbound trap from the 12 sites in the project. Data points falling outside the whiskers are considered outliers and are depicted here as the solid black dots.



Figure 3.4 Abundance of Saproxylic families and their correlation with connectivity. The Y-axis displays the abundance, and the X-axis represents the total volume of spruce trees within the specified radius around the sites. Connectivity is measured in (m³). The trendline indicates a positive correlation with connectivity for all three families.

3.3 Abundance of Selected Saproxylic Families

The candidate models with the best AIC-values for Mycetophilidae, Chironomidae, and Syrphidae was the zero model. Consequently, the models did not consider any of the predictor variables as a good fit to describe any variation in abundance among the three families (App. B, Table B29-34).

3.3.1 Effects of Forest Type

Forest type had a significant effect on the abundance of some Diptera families. There was evidence for a higher abundance of phorids (p = 0.022, Fig. 3.5) in mature clear-cut forests (App. B, Table B5,B6), weak evidence for a higher abundance of Limoniidae (p = 0.096, Fig. 3.6) in mature clear-cuts, whereas abundance of Pipunculidae (p = 0.088, Fig. 3.6) was highest in near-natural forests (App. B, Table B7-B10).



Figure 3.5. Boxplot showing the abundance of Phoridae in near-natural and mature clear-cut forest, for period 1 and 3. Each data point is shown as a faded dot, which represent each northbound trap from the 12 sites in the project. Data points falling outside the whiskers are considered outliers and are depicted here as the solid black dots.



Figure 3.6 Boxplot showing the abundance of Pipunculidae (to the left) and Limoniidae (to the right) for both forest types (CC and NN) across period 1 & 3. Each data point is shown as a faded point, which represent each northbound trap from the 12 sites in the project. Data points falling outside the whiskers are considered outliers and are depicted here as the black solid points. There was evidence for a higher abundance in CC than in NN.

3.3.2 Effects of Dead Wood

For Tipulidae abundance there was evidence for a correlation with dead wood volume (p = 0.042) (Fig. 3.7). There was also weak evidence between Empididae abundance and dead wood volume (p = 0.071)(Fig. 3.7). No other families among the saproxylic Diptera had a significant realtionship with dead wood. Results from the GLMM and the AIC-values can be found in App. B, B11-B14.



Figure 3.7 Abundance of Tipulidae and Empididae and their correlation with dead wood. The Y-axis displays the abundance, and the X-axis represents the total dead wood volume (m³). The trendline indicates a correlation with dead wood for both families.

3.3.3 Effects of Connectivity

Effects on connectivity were also discovered (Fig. 3.8). Anthomyiids displayed a strong evidence (p = 0.008) of correlation between higher abundance and increased connectivity. For Phoridae (p = 0.022) and Fanniidae (p = 0.023) there was evidence of higher abundance with increased connectivity (Fig. 3.8). Results from the GLMM and the AIC-values can be found in App. B, B5,B6, B15-B18.



Figure 3.8. Abundance of Anthomyiidae, Phoridae, and Fanniidae and their correlation with connectivity. The Y-axis displays the abundance, and the X-axis represents the total volume of spruce trees within the specified radius around the sites. Connectivity is measured in (m³). The trendline indicates a correlation with connectivity for all three families.

3.3.4 Effects of Period, Temperature and Precipitation

Several Diptera families differed in abundance in period 1 compared to period 3 (Fig. 3.9). There was very strong evidence (p < 0.001) for this for Anthomyiidae, Muscidae, Empididae, Tipulidae, Tachinidae, Hybotidae, as well as evidence for Sciaridae (p = 0.011), Phoridae (p = 0.026), Limoniidae (p = 0.044), and Fanniidae (p = 0.031). While most of them where more abundant in periode 3, the opposite was true for the Scaridae.

Several families were influenced by weather variables. Phoridae abundance showed evidence for a correlation with mean temperature (p = 0.038). Sciaridae abundance was positively correlated with precipitation (p = 0.025). Dolichopodidae abundance displayed weak evidence for a correlation with mean precipitation (p = 0.062). For Tachinidae, there was strong evidence of a correlation with mean precipitation (p = 0.006) and additional evidence

Results from the GLMM and the AIC-values can be found in App. B, B5-B8, B11-26.



Figure 3.9 Boxplot showing the abundance of Sciaridae, Anthomyiidae, Empididae, Muscidae, Hybotidae, Tachinidae, Fanniidae and Tipulidae in near-natural and mature clear-cut forest, for period 1 and 3. Each data point is shown as a faded dot, which represent each northbound trap from the 12 sites in the project. Data points falling outside the whiskers are considered outliers and are depicted here as the solid black dots.

4. Discussion

The initial sorting process revealed that the proportion of Diptera (without Sciaridae) was higher than Hymenoptera, and Coleoptera (Fig. 3.1.). This aligns with findings of previous master students in EcoForest, and studies such as the Swedish Malaise trap project (Karlsson et al., 2020). However, identification to family-level uncovered that a big proportion of Diptera were Sciaridae. If they are ignored, the proportion among orders changes completely as Hymenoptera becomes the dominant order. Ultimately, Diptera might still be the most abundant order since I had to remove the Cecidomyiidae from the analyses, due to identification issues. I also suspect a lot of the unidentified Diptera were Chironomidae.

These families, the Chironomidae, Cecidomyiidae, and Sciaridae, are all known to be very common Diptera (Courtney et al., 2017; Karlsson et al., 2020), and the latter two are very common in forest soil (Frouz, 1999). This further supports my assumption, based on my findings, that Diptera are the dominant order of insects in these forest ecosystems.

41. Effects of Forest Management

I expected to find a greater abundance of Diptera in near-natural forests. However, neither total Diptera abundance, nor total number of saproxylic Diptera differed significantly (H1) between the two forest types. Only Pipunculidae (p = 0.088) displayed this pattern, while higher numbers of Phoridae (p = 0.014) and Limoniidae (p = 0.096) was found in mature clear-cut forests.

A possible explanation for the outcome regarding Diptera both as an order and as a saproxylic group might be the broad ecological diversity within the order, encompassing species with a wide range of habitat requirements (Ulyshen, 2018). For instance, many Mycetophilidae require fungi to fulfill their life history (Økland, 1996), some species of Scathophagidae lay eggs in animal dung (Šifner, 2008), and most Tachanidae operates as parasitoids on other insects (Grenier, 1988; Stireman III et al., 2006). The ecology also vary within families (Ulyshen, 2018), making uniform responses unlikely and existing difference difficult to detect. The classification of certain families as saproxylic generalises their ecological roles, as they display many life strategies and utilise various substrates, potentially leading to non-uniform responses.

Phoridae and Limoniidae are known to include saproxylic species (Ulyshen, 2018), however, these families were found in greater abundance in mature clear-cut forests. Similar to this, Durska (2013) reported higher populations of smaller saprotrophic and mycophagous phorids in fresh clear-cuts compared to undisturbed forests. Altough my study focused on mature clear-cuts, long-term effects from clear-cutting on current populations of Diptera might still be evident. Økland (1994) demonstrated such persistent effects of clear-cutting on Mycetophilidae diversity, with no recovery observed even 70 - 120 years later, which emphasises the major long-term impact this forestry practise may have on the ecosystems.

Some phorids favour habitats with natural disturbance regimes (Durska, 2013), and if there still is persistent effects from past disturbances in the mature clear-cuts, there might be unknown aspects of these areas influencing their abundance. The phorids from the mature clear-cuts in my study might prefer saprophytic fungi, which positively responds to clear-cut events (Rähn et al., 2023).

Some phorids are also known to be parasitoids of Sciaridae (Durska et al., 2010; Durska, 2013), which were particularly numerous in the mature clear-cuts. If many of the phorids in my findings are parasitoids of Sciaridae, their presence aligns with the understanding that parasite populations are closely tied to the availability of hosts (Crawley, 1975). However, this remains unknown as phorids were only identified to the family level.

Given the broad diversity within the Limoniidae family, it is difficult to determine why they were more numerous in the mature clear-cut compared to the near-natural forests. Globally, there are more than 1100 species (Savchenko et al., 1992), while in Norway, 197 species have been documented, all of which are classified as limnic (Artsdatabanken, 2020).

A study by Theenhaus & Schaefer (1995) on effects of clear-cutting and liming on soil macrofauna, found that the emergence of Limoniidae was significantly higher in clear-cuts compared to the control forest plot. The main assumption in the study was that the change of soil moisture due to clear-cutting influenced most of the sampled populations, as 7% more precipitation reached the ground in the clear-cuts compared to the other forest plots. This is essential for most Limoniidae larvae, as they require wet conditions to live (Olsen et al., 2018; Savchenko et al., 1992; Ševčík, 2006; Solem & Mendl, 1989).

The study by Theenhaus & Schaefer (1995) was conducted in a beech forest within a 3 year old clear-cut, which limits direct comparison with the mature spruce clear-cuts analysed in my study. If the soil in mature clear-cuts are better at absorbing precipitation than near-

natural forests, this might be one reason for the higher number of Limoniidae found in that forest type.

The mature clear-cut forest at Langvassbrenna was the site where the highest number of Limoniidae were caught, accounting for 29% of the total catch. The Malaise traps were installed in close proximity to the lake, Fagervannet (~200 m), a habitat potentially facilitating for Limoniidae. However, Limoniidae larvae do not necessarily require open water for their development. They can also thrive in semi-aquatic habitats such as marshes, moist soil, decaying vegetation, and forests (Savchenko et al., 1992), which also were present in the area.

Although not statistically significant, the majority of Pipunculidae (80%) showed a weak evidence towards a correlation with near-natural forests. Among the Pipunculidae in my samples, 32 were found in near-natural forests, and only 8 in the mature clear-cuts. This might also be a coincidence, but there are some evidence supporting their preference to older forest.

A study by Kehlmaier and Floren (2010) used canopy fogging to sample Pipunculidae in Polish forests, collecting 386 specimens from various tree-dominated stands and forest ages. *P. abies* supported the highest number of specimens, while primeval forests, which included all tree types, had the greatest total count. The study did not address clear-cutting specifically, but it did mention that all forests, except the primeval were managed. The preference of Pipunculidae for forest openings and greater gap dynamics in older forests (McCarthy, 2001), may help understand why they were more numerous in near-natural forests compared to the mature clear-cuts.

Most Pipunculidae are parasitoids on Auchenorrhyncha except the genus *Nephrocerus* which targets adult Tipulidae (Crany flies) of the genus *Tipula* (De Meyer et al., 2021; Kehlmaier & Floren, 2010; Kvifte, 2011; Withers & Claude, 2021). Understanding the habitat requirements of Auchenorrhyncha and *Tipula*, particularly whether they prefer older spruce forests, would be valuable as it could indirectly enhance our knowledge of Pipunculidae.

While the number of Sciaridae was considerably higher in the mature clear-cuts compared to near-natural forests (Fig. 3.9), the statistical analysis could not find that forest type had a significant effect on Sciaridae abundance. This might be due to the large variation of Sciaridae abundance within the mature clear-cut sites.

Sciaridae populations have been observed to decline with forest maturity due to changes in soil conditions (Frouz, 1999). Their high abundance in mature clear-cut sites, despite being clear-cut 70 years ago, suggests that even decades after the disturbance event, the soil conditions in these areas can still support large numbers of Sciaridae. In contrast, the near-natural forest, never subjected to clear-cutting, had much lower Sciaridae numbers. This aligns with the idea that Sciaridae decline is related to forest maturity.

42. Effects of Dead Wood

While the quantity of dead wood varies considerably between forest types, there is also substantial variation among the different sites within the study. Treating dead wood as a continuous variable could therefore provide a clearer picture of the importance of dead wood compared to forest type. I expected to find a greater abundance of Diptera correlated with higher volumes of dead wood. However, I found no statistically significant correlation between the amount of dead wood and abundance of neither total Diptera, nor saproxylic Diptera as a group. I did however find a significant correlation with one individual family – the Tipulidae (p = 0.042), and a weak evidence for a correlation with Empididae (p = 0.071).

The lack of correlation to dead wood might be attributed to dominant species not responding directly to the amount of dead wood. The knowledge about certain saproxylic Diptera is insufficient, and other substrates might be more relevant than dead wood. An example of this is the species *Tipula (Pterelachisus) laetibasis,* which initially was believed to be saproxylic, but later found to be more closely associated with humus-rich soil (Salmela, 2009). Some Diptera that also rear their larvae in wood-decaying fungi may also utilise other substrates, such as non-saproxylic mycorrhizal fungi. While these Diptera may prefer dead wood, they are not necessarily dependent on it. Those that can use alternative substrates are known as *facultative* saproxylics, in contrast to *obligate* saproxylics, which rely exclusively on dead wood (Stokland et al., 2012).

Variations among species across different stages of dead wood decay could potentially mask any observable differences. Dead wood at the various sites was categorized into five stages of decay according to Stokland et al., (2012), but the statistical tests did not support this level of complexity. Irmler et al., (1996) found that Sciaridae and Mycetophilidae were more abundant, particularly in old and decayed wood. Future research should, therefore, consider the decay stage of dead wood and, ideally, identify the species rather than just the families.

There are some evidence that microhabitats and earlier decay stages of dead wood are more important for some Diptera, than old forests (Rotheray et al., 2001), which support larger volumes of dead wood and several decay classes. This could also be the case for the diverse Tipulidae, which are found in many different habitats (Freeman, 1967; Oosterbroek & Theowald, 1992). The larvae of Tipuloids can be found in dead wood, moss, liverworts, soil, leaf litter, marshes and fungi – often in moist habitats (Oosterbroek & Theowald, 1992). These habitats are not restricted to either one of the nature types in my study, and both have the potential to support species of Tipulidae.

Due to the low sample size of Tipulidae (35 individuals) and the nearly identical distribution between the mature clear-cut (19 individuals) and near-natural forests (16 individuals), it is challenging to determine the significance of dead wood distribution, especially without further identification of Tipulidae.

Research on Tipulidae is more extensive in Finland compared to Norway, but the shared forest characteristics between Norway and Finland suggest potential similarities in species distribution. A few saproxylic species occuring in Finland, are also found in Norway, such as *Tipula cinereocincta*, *T. pseudoirrorata*, *T. wahlgreni*, and *T. irrorata* – a very common saproxylic Palaearctic species (Salmela, 2009). Many observations of it comes from southeastern Norway (Artsdatabanken, 2021b), and is reared from both *Populus tremula* (Aspen) and *P. abies* (Salmela, 2009).

Discussions about the importance of coarse woody debris (CWD) and associated fungal diversity could also be relevant for some fungivorous Tipulidae, as fungivore abundance were correlated with CWD (Ulyshen, 2018; Vanderwel et al., 2006). While not the single determining factor, this also influenced Mycetophilidae abundance in Økland (1996), where timber removal reduced the diversity of wood-inhabiting fungi – an important substrate for mycetophilids (Søli, 2017; Ulyshen, 2018; Økland, 1994).

Empididae are primarily known as predators (Chandler, 1978; Cumming & Sinclair, 2009; Cumming et al., 2018), although some species display saprophagous behaviour in decaying wood (Ulyshen, 2018). A few are also found on bark, and decaying sap or sapwood (Rotheray et al., 2001). Larval habitats involve diverse environments, including moist soil, dung, mosses and decaying wood. Many larvae also predate other insect larvae (Chandler, 1978; Cumming & Sinclair, 2009; Grootaert, 2004), but the Empididae larval stage remains relative understudied (Chandler, 1978). According to my hypothesis, there was weak evidence (p = 0.071) between Empididae abundance and dead wood volume. The weak correlation with higher volumes of dead wood might be due to predation of other saproxylic insects who thrive on this substrate. In Ireland, many of the Empididae living in forests, are found on trunks or among the leaves on trees (Chandler, 1978).

Many of the Empididae described by Chandler (1978) have in later years been moved to the family Hybotidae – for instance the two genera, *Oropezella* and *Euthyneura*, and the species *Leptopeza flavipes*, which all are affiliated with decaying wood. Still, none of the Hybotidae in my samples displayed any correlation with dead wood.

The relationship between Empididae and dead wood remains relatively understudied, despite the predatory nature of many species, and the association of some with decaying wood. Both adult and larva likely prey on other saproxylic insects, but many are either obligate or facultative in their affinity for dead wood (Cumming et al., 2018). If saproxylic insects constitute a substantial portion of local ecosystems, the importance of dead wood for Empididae might be greater than currently assumed. Further research is necessary to clarify the specific role of dead wood in the life history of Empididae.

4.3 Effects of Connectivity

Supporting the initial hypothesis, a positive correlation was found between the abundance of Anthomyiidae (p = 0.008), Phoridae (p = 0.022), and Fanniidae (p = 0.023), and the connectivity of living spruce trees older than 80 years (Fig. 3.8). No other families or group of Diptera were significantly correlated with habitat connectivity.

Many Diptera, including some Anthomyiidae, rely on specialized microhabitats, such as decaying sap, sapwood, and sap exudations (Griffiths, 1997; Rotheray et al., 2001). The availability of continuous microhabitats with abundant resources, can be necessary for the survival and development of many larvae, as well for adult feeding (Griffiths, 1997; Rotheray & Rotheray, 2019; Ulyshen, 2018)(Rotheray & Rotheray, 2016; Griffiths, 1997; Ulyshen, 2018). This is why ensuring habitat connectivity can be important for maintaining these microhabitats (Rotheray et al., 2001; Wolton & Luff, 2016).

Phorid communities in pine forests have proved to change and increase in species diversity with secondary succession and older tree stands, even though they stabilise over time (Durska, 2001). There is also evidence for greater species diversity in old growth pine forests, compared to plantation forests and post-windstorm areas, as Durska (2013) uncovered. In that same study, there was also a correlation between body size and habitat preference in phorids, where larger species preferred more intact old-growth forests compared to areas of disturbance, such as clear-cuts (Durska, 2013). Although there is little knowledge on the same dynamics for phorids in spruce forests, similar patterns are most likely to occur due to the importance of fungi and dead wood for many phorids (Ulyshen, 2018).

To my knowledge, information on the distribution and habitat requirements on Fanniidae in Fennoscandia is limited, which made the assessment of their correlation with habitat connectivity challenging. Many species of Fanniidae display saprophagous behaviour while feeding on carrion (Grzywacz et al., 2018). This suggests a potential connection between Fanniidae abundance and the total abundance of vertebrate and invertebrate carrion within an ecosystem. Additionally, some Fanniidae species utilise bird nests or nest of various Hymenoptera during their larval stage (Rozkošný, 1997). Considering the association with many saproxylic Hymenoptera and dead wood (Hilszczański et al., 2005), indirect connections between Fanniidae and dead wood may exist.

4.4 Effects of Period, Temperature & Precipitation

The study revealed a significant increase of Total Diptera abundance in period 3 (Fig. 3.2), with specific saproxylic Diptera like Phoridae (Fig. 3.6), Empididae, Muscidae, and Hybotidae (Fig. 3.9) also showing this pattern. In contrast, the Sciaridae displayed a much greater abundance in period 1 compared to period 3.

Prior to emergence in spring, dipterans must wake up from their diapause, which is a state of dormancy that allows them to survive over the winter. Springtime emergence is triggered by a combination of increasing temperatures and day length, signaling favorable conditions for development and reproduction (Danks, 2007). The trap installation may have begun before the emergence of most Diptera, which could explain why the first period captured fewer flies. This assumption was somehow reinforced at site 12 (Langvassbrenna), where patches of snow were still present during the trap assembly. Many insects also synchronize their development to emerge at different times, as a strategy to avoid competition, or synchronize them with the blooming of specific flowers they depend on (Danks, 2007). This is why a different distribution of insects can occur at different times. This emphasises the importance of gathering data at multiple time points.

Since insects are ectotherms, they are influenced by their environment. This means that weather can influence the pattern of emergence (Danks, 2007). Sciaridae abundance displayed a significant correlation with mean precipitation, suggesting a reduction in abundance in wetter forests stands. Dolichopodidae showed a weak trend, indicating a slight increase in abundance from higher precipitation.

4.5 Improvements and future research

4.5.1 Species-level identification

Species-level identification is essential, as family-level identification may lack the detail needed to accurately assess ecological variation, substrate preferences, habitat selection, or specific behaviours within families. However, manually identifying Diptera can be quite challenging due to factors such as insufficient identification keys, large sample sizes, and the high diversity of species, many of which are either poorly understood or closely resemble each other. A recent paper suggests that specimen photography and DNA metabarcoding, holds great promise for progress in species identification, and evaluations of abundance and biomass (Sickel et al., 2023). Still, the current limitations to this are the lack of comprehensive reference libraries (Watts et al., 2019).

4.5.2 Collection period

Analysing data from only two collection periods, despite collecting samples across four, highlights the time limitations of manual identification within a two-semester timeframe. If I had analysed the samples from all periods, it would have provided a much more comprehensive view of the distribution over time. I might have found more individuals, which could have revealed a different outcome.

4.5.3 Trap considerations

Utilising only one type of Malaise trap might have introduced bias into the data. These traps can favour specific Diptera families, genera, or even species. Since Malaise traps function as interception traps, they may not be the most effective method for capturing skilled fliers like many Syrphidae and Pipunculidae, which often evade them (De Meyer & De Bruyn, 1989). Furthermore, Malaise traps are typically installed on the ground and may only catch species that fly at lower levels. Maguire (2014) found that Diptera abundance and diversity were significantly higher in the forest canopy, with species composition differing between canopy and ground levels. This was also supported by Ruchin et al., (2024), which caught different

Diptera at multiple heights with beer traps. Although not statistically significant, the majority of Syrphidae in that study was caught 12 meter above ground. The same applied for Lonchaeidae, Anthomyiidae, Fanniidae, and Muscidae.

Several of the families caught in the Malaise traps, such as Tipulidae, Anisopodidae, Anthomyiidae, Drosophilidae, Fanniidae, and Muscidae, are attracted to sap secretion. This substance is affiliated with saproxylic Diptera, and in order to sample more of them, trapping methods using beer or sugar-containing ingredients (Ruchin et al., 2024), in addition to the malasie traps, could prove to be more efficient than using the Malaise traps alone.

4.5.4 Sample treatment

DNA was extracted from the Diptera specimens for further analysis with DNA metabarcoding, for a parallel study in EcoForest. However, the lysis buffer used to extract the DNA, caused some damage to key anatomical features used for morphological identification. This was particularly noticeable for Cecidomyiidae and Chironomidae, where the damaged wing structures and antennae made it difficult to accurately identify them.

4.5.5 Unknown predictors

Improvement of collection parameters and species identification might provide a broader perspective of the effect of forest type on Diptera abundance. However, other unknown predictor variables in the forest types, might have an impact on Diptera abundance. Most families within the saproxylic group have the potential to utilise other substrates than dead wood, and none of the identified families exhibit exclusive saproxylic characteristics (Ulyshen, 2018). Rotheray et al., (2001) found that specific stages of decay in microhabitats were important, such as decaying sap between the bark and sapwood. In addition, not all Diptera rely directly on dead wood, but indirect affiliation can also be important as one study by Hövemeyer & Schauermann (2003), observed that increased moss cover on dead wood correlated with species density of certain hygrophilous families.

A Swedish study also found that nearly a third of saproxylic insects exhibited some degree of host specificity (Jonsell et al., 1998). This has also been the assumption for Diptera. However, research suggests a that microhabitats such as decaying sap between the bark and sapwood might be more important (Rotheray et al., 2001). This implies that specific decay stages, not necessarily restricted to old-growth forests, might be more essential for Diptera abundance than the presence of old spruce trees themselves. The decaying sap between the

bark and sapwood is accessible for about 3 years after the wood have fallen to the ground, until air dried out the sap. Consequently, to maintain sufficient microhabitat availability, a continuous input of fallen or cut wood is necessary every 1-3 years (Rotheray et al., 2001). While this do not explain the increase of certain Diptera families in the mature clear-cut, it emphasises that the factors influencing Diptera distribution and abundance is complex.

To improve the accuracy of assessments, targeting the breeding sites of specific species or families through larval sampling can also be done. Diptera diversity is often linked to larval feeding behaviour (Courtney et al., 2017). Microhabitats such as rot holes in pine trees are almost always accessible for sampling as the larva have several growth stages spanning more than a year (Rotheray et al., 2001). This methodology demands a very thorough knowledge of larvae ecology.

Sciaridae are among the most common and numerous Diptera found in forests, often associated with soil . Their larvae inhabit soil litter, where they feed on plant roots and decomposing organic matter, contributing significantly to nutrient cycling within forest ecosystems . The larvae's saprophagous life strategy suggests that increased litter after a clear-cut event might enhance their numbers, explaining their proliferation. However, this effect may only be significant during the first few years after clear-cutting. Without a comparable sampling from a fairly fresh clear-cut, I cannot determine whether the decline in their population is linear with forest maturity.

5. Conclusion

In this thesis the abundance of Diptera was investigated as a response to long-term influence of forest management types - mature clear-cut and near-natural spruce forest. The predictor variables dead wood and habitat connectivity are closely associated to near-natural forests and has previously been identified to be important for other insect orders. These predictors, and collection period, precipitation, and temperature were evaluated to assess the effect on abundance of total Diptera, saproxylic Diptera and selected saproxylic families.

The results revealed few differences in abundance between mature clear-cuts and near-natural forests, except for Phoridae (evidence) and Limoniidae (weak evidence), that were more abundant in mature clear-cuts, and Pipunculidae (weak evidence) that were more abundant in near-natural forests.

Contrary to other studies on the insect order Coleoptera, dead wood was only correlated with Tipulidae (evidence) and Empididae (weak evidence).

Connectivity was positively correlated with saproxylic families as a group, as well as some selected families (Phoridae, Anthomyiidae and Fanniidae).

The lack of significant differences between the forest types, as well as correlation between dead wood and connectivity for most Diptera families, might be attributed to dominant species not responding to the predictor variables tested, but it may also be attributed to variation in the responses from different Diptera species that masked detectable differences.

A better understanding of Diptera is essential to develop potentially needed mitigation strategies and guide future conservation efforts for both the insects and important forest habitats. Therefore, future studies could try different traps, extend the sampling period, and include other predictor variables such as fresh dead wood decay. However, the most promising approach is to include DNA metabarcoding to overcome challenges in Diptera species identification.

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Appendix A (Sites, variables and model selection)

A1. Overview of trap sites

Table A.1 Overview of all trap sites, including their location ID, associated forest types, and designated trap collection intervals. Additional comments are included.

Location name	Location	Forest	Installing traps	Period 1	Period 2	Period 3	Period 4	Comments
	number	Туре						
Skotjernfjell	1	NN	25.05.2022	09.06.2022	22.06.2022	05.07.2022	20.07.2022 & 21.07.2022	It was emptied again 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 again 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 again 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 again on 03.08.2022
Hemberget	3	NN	30.05.2022	12.06.2022	24.06.2022	08.07.2022	25.07.2022 & 27.07.2022	It was emptied again on 06.08.2022
Hemberget	3	CC	30.05.2022	12.06.2022	24.06.2022	08.07.2022	25.07.2022 & 27.07.2022	It was emptied again on 06.08.2022
Braskeidfoss	4	NN	31.05.2022	13.06.2022	27.06.2022	08.07.2022	26.07.2022	It was emptied again on 07.08.2022
Braskeidfoss	4	CC	31.05.2022	13.06.2022	27.06.2022	08.07.2022	26.07.2022	It was emptied again 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 again 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 again 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 again 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 again 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 again 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 again 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 again 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 again 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 again 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 again 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 again 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 again 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	

A2. Overview of Diptera family and count

Table A.2 Overview of the identified Diptera families in the order of most abundant to least abundant.

Families of Diptera	CC	NN	Period 1	Period 3	Total count
Sciaridae	11128	5551	14318	2361	16679
Phoridae	711	363	494	580	1074
Mycetophilidae	249	201	206	244	450
Anthomyiidae	157	220	17	360	377
Empididae	110	145	23	232	255
Muscidae	82	126	18	190	208
Hybotidae	71	126	19	178	197
Scathophagidae	43	58	6	95	101
Chironomidae	49	48	77	20	97
Dolichopodidae	43	37	8	72	80
Syrphidae	27	40	21	46	67
Tachinidae	31	32	17	46	63
Simuliidae	40	11	34	17	51
Pipunculidae	8	32	8	32	40
Fanniidae	7	31	4	34	38
Tipulidae	19	16	1	34	35
Limoniidae	26	9	13	22	35
Rhagionidae	10	16	0	26	26
Lauxaniidae	15	11	2	24	26
Ceratopogonidae	11	12	1	22	23
Psychodidae	6	14	0	20	20
Clusiidae	5	5	0	10	10
Anisopodidae	3	6	8	1	9
Psilidae	2	7	0	9	9
Drosophilidae	4	3	3	4	7
Pediciidae	2	5	0	1	1
Tabaridae	4	2	1	5	5
	4	1	0	3	5
	2	3	4	1	5
Cylindrotomidae	2	2	3	2	3
Heleomyzidae	2	1	1	3	4
Chaoboridae	0	3	3	0	3
Strongylophthalmyiidae	0	3	0	3	3
Sphaeroceridae	2	1	2	1	3
Xvlophagidae	3	0	0	3	3
Oestridae	1	1	0	2	2
Ditomyiidae	2	0	0	2	2
Rhinophoridae	2	0	0	2	2
Carnidae	1	0	0	1	1
Keroplatidae	0	1	0	1	1
Trichoceridae	1	0	1	0	1
Lonchaeidae	1	0	1	0	1
Ptychopteridae	0	1	0	1	1
Stratiomyidae	0	1	0	1	1
Mycetobiidae	1	0	0	1	1

A3. Predictor information

Table A.3. Showing the predictor variables in my study together with an explanation of what they are, and where I obtained some of them.

Independent variables	Explanation
Mean temperature (°C)	From TOMST loggers at sites
Mean precipitation	Data from the Norwegian Meteorological Institute
Connectivity	Connected forest (80 years), average spread (0.5km)
Year	10 sample locations (2022), 2 sample locations (2023)
Period	Period 1 & Period 3, "see Appendix A for a complete overview."
Forest Type	Forest management type. Either near-natural (NN) or clear-cut (CC).
Total dead wood volume	Total volume (of dead wood, both standing snags and downed dead wood, and all decay
	classes.

A4. Degree of significance

Table A.4. The degrees of significance used to describe the p value for the predictors (Muff et al., 2022).

Degree of evidence	<i>P</i> value
Little or no evidence	Greater than 0.1
Weak evidence	Between 0.05 and 0.1
Evidence	Between 0.01 and 0.05
Strong evidence	Less than 0.01
Very strong evidence	Less than 0.001

Appendix B - Generalized Linear Mixed Model Results

B.1 Total Diptera

Table B.1 Poisson distributed, generalised linear mixed model with log link for abundance of Total Diptera(without Sciaridae). Site was used as a random effect together with an observation-level random effect (OLRE)to account for variation not explained by the predictors. Statistically significant values are marked in bold.Additional details on the predictors are found in Appendix A, Table A.3.

Total Diptera Abundance (Model 6)					
	Estimate	SE	z-value	<i>p</i> -value	
Intercept	3.5678	0.2468	14.456	P < 0.001	
Forest type (NN)	-0.3745	0.2705	-1.385	0.166	
Period (3)	1.3002	0.2484	5.235	P < 0.001	
Year (2023)	1.0868	0.4024	2.701	0.007	
Connectivity	0.2779	0.1552	1.791	0.073.	

Table B.2 AIC Results for Total Diptera (without Sciaridae). The best model is highlighted in bold.

Diptera without Sciaridae					
	df	AIC			
Model 0	3	565.816			
Model 1	10	550.239			
Model 2	9	548.320			
Model 3	8	549.573			
Model 4	6	546.851			
Model 5	7	547.789			
Model 6	7	545.707			

B.2 Saproxylic Diptera

Table B.3 Poisson distributed, generalised linear mixed model with log link for abundance of Saproxylic Diptera (without Sciaridae). Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Saproxylic Diptera (Model 6)					
	Estimate	SE	z-value	<i>p</i> -value	
Intercept	3.3130	0.2381	13.912	P < 0.001	
Forest type (NN)	-0.3953	0.2486	-1.590	0.112	
Period (3)	1.0020	0.2240	4.474	P < 0.001	
Year (2023)	0.5614	0.4141	1.356	0.175	
Connectivity	0.4406	0.1540	2.861	0.004	

Table B.4 AIC Results for Saproxylic Diptera (without Sciaridae). The best model is highlighted in bold.

Saproxylic Diptera (Model 6)					
	df	AIC			
Model 0	3	506.2796			
Model 1	10	496.2397			
Model 2	9	495.0328			
Model 3	8	499.4468			
Model 4	6	496.0340			
Model 5	7	495.6869			
Model 6	7	491.2925			

B3. Phoridae

Table B.5 Poisson distributed, generalised linear mixed model with log link for abundance of Phoridae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Phoridae – Model 1					
	Estimate	SE	z-value	<i>p</i> -value	
Intercept	1.8362	0.4254	4.316	P < 0.001	
Forest type (NN)	-0.7163	0.2905	-2.466	0.014	
Period (3)	1.5385	0.6893	2.232	0.026	
Year (2023)	1.3425	0.5874	2.285	0.022	
Mean precipitation	0.1624	0.2567	0.633	0.527	
Mean temperature	-0.7209	0.3477	-2.073	0.038	
Connectivity	0.3896	0.1703	2.287	0.022	

Table B.6 AIC Results for Phoridae. The best model is highlighted in bold.

Phoridae - Model 1						
	df	AIC				
Model 0	3	393.344				
Model 1	10	390.408				
Model 2	9	391.161				
Model 3	8	393.312				
Model 4	6	393.330				
Model 5	7	393.774				
Model 6	7	390.472				

B4. Limoniidae

Table B.7 Poisson distributed, generalised linear mixed model with log link for abundance of Limoniidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Limoniidae – Model 4				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-1.7686	0.7003	-2.525	0.012
Forest type (NN)	-1.0747	0.6464	-1.663	0.096.
Period (3)	1.3875	0.6890	2.014	0.044
Year (2023)	0.8005	0.7544	1.061	0.289

Table B.8 AIC Results for Limoniidae. The best model is highlighted in	bold
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Limoniidae - Model 4		
	df	AIC
Model 0	3	111.542
Model 1	10	112.438
Model 2	9	110.752
Model 3	8	109.740
Model 4	6	109.510
Model 5	7	109.983
Model 6	7	111.030

B.5 Pipunculidae

Table B.9 Poisson distributed, generalised linear mixed model with log link for abundance of Pipunculidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Pipunculidae – Model 4				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-3.0889	0.9039	-3.417	P < 0.001
Forest type (NN)	1.2524	0.7339	1.707	0.088.
Period (3)	1.0859	0.7213	1.506	0.132
Year (2023)	1.0696	0.8644	1.237	0.216

Table B.10 AIC Results for Pipunculidae. The best model is highlighted in bold.

Pipunculidae - Model 4				
	df	AIC		
Model 0	3	111.124		
Model 1	10	113.570		
Model 2	9	111.572		
Model 3	8	111.936		
Model 4	6	110.862		
Model 5	7	112.214		
Model 6	7	112.010		

B.6 Tipulidae

Table B.11 Poisson distributed, generalised linear mixed model with log link for abundance of Tipulidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Tipulidae – Model 5				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-3.07658	1.04806	-2.935	0.003
Forest type (NN)	-0.59976	0.48157	-1.245	0.213
Period (3)	3.50895	1.02855	3.412	P < 0.001
Year (2023)	0.06515	0.58156	0.112	0.911
Total dead wood volume	0.37441	0.18423	2.032	0.042

Table B.12 AIC Results for Tipulidae. The best model is highlighted in bold.

Tipulidae - Model 5		
	df	AIC
Model 0	3	116.367
Model 1	10	102.804
Model 2	9	103.823
Model 3	8	102.763
Model 4	6	99.156
Model 5	7	97.865
Model 6	7	99.925

B.7 Empididae

Table B.13 Poisson distributed, generalised linear mixed model with log link for abundance of Empididae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Empididae – Model 5	_			
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-1.1799	0.5543	-2.129	0.033
Forest type (NN)	-0.1720	0.5404	-0.318	0.750
Period (3)	2.6064	0.5191	5.020	P < 0.001
Year (2023)	1.1807	0.6073	1.944	0.052.
Total dead wood volume	0.4524	0.2504	1.807	0.071.

Table B.12 AIC Results for Empididae. The best model is highlighted in bold.

Empididae - Model 5		
	df	AIC
Model 0	3	250.942
Model 1	10	237.868
Model 2	9	238.699
Model 3	8	237.205
Model 4	6	233.501
Model 5	7	232.315
Model 6	7	234.878

B.8. Anthomyiidae

Table B.15 Poisson distributed, generalised linear mixed model with log link for abundance of Anthomyiidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Anthomyiidae – Model 6				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-1.2123	0.5496	-2.206	0.027
Forest type (NN)	-0.5672	0.5220	-1.087	0.277
Period (3)	3.3853	0.5519	6.133	P < 0.001
Year (2023)	0.5878	0.6331	0.928	0.353
Connectivity	0.6952	0.2636	2.638	0.008

Table B.16 AIC Results for Anthomyiidae. The best model is highlighted in bold.

Anthomyiidae - Model 6		
	df	AIC
Model 0	3	274.178
Model 1	10	248.224
Model 2	9	246.844
Model 3	8	245.320
Model 4	6	246.614
Model 5	7	247.285
Model 6	7	244.886

B.9 Fanniidae

Table B.17 Poisson distributed, generalised linear mixed model with log link for abundance of Fanniidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Fanniidae – Model 6				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-4.84577	1.60388	-3.021	0.003
Forest type (NN)	0.53389	1.06458	0.501	0.616
Period (3)	2.41932	1.12307	2.154	0.031
Year (2023)	0.05883	1.35676	0.043	0.965
Connectivity	1.94606	0.85604	2.273	0.023

Table B.18 AIC Results for Fanniidae. The best model is highlighted in bold.

Fanniidae - Model 6			
	df	AIC	
Model 0	3	93.253	
Model 1	10	95.400	
Model 2	9	93.424	
Model 3	8	98.039	
Model 4	6	96.369	
Model 5	7	97.062	
Model 6	7	90.650	

B.10 Muscidae

Table B.19 Poisson distributed, generalised linear mixed model with log link for abundance of Muscidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Muscidae – Model 4				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-1.28686	0.51670	-2.491	0.013
Forest type (NN)	0.64864	0.41451	1.565	0.118
Period (3)	2.24750	0.44128	5.093	P < 0.001
Year (2023)	0.04988	0.78999	0.063	0.950

Table B.20 AIC Results for Muscidae. The best model is highlighted in bold.

Muscidae - Model 4		
	df	AIC
Model 0	3	233.881
Model 1	10	223.756
Model 2	9	222.295
Model 3	8	220.509
Model 4	6	218.936
Model 5	7	220.044
Model 6	7	220.336

B.11 Tachinidae

Table B.21 Poisson distributed, generalised linear mixed model with log link for abundance of Tachinidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Tachinidae – Model 3	-			
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-1.5896	0.6022	-2.640	0.008
Forest type (NN)	-0.2791	0.3480	-0.802	0.422
Period (3)	3.0557	0.8606	3.551	P < 0.001
Year (2023)	-0.8058	0.8238	-0.978	0.328
Mean precipitation	-0.8566	0.3087	-2.775	0.006
Mean temperature	-0.8500	0.4305	-1.974	0.048

Table B.22 AIC Results for Tachinidae. The best model is highlighted in bold.

Tachinidae - Model 3			
	df	AIC	
Model 0	3	151.427	
Model 1	10	148.846	
Model 2	9	147.643	
Model 3	8	146.458	
Model 4	6	153.373	
Model 5	7	155.343	
Model 6	7	155.148	

B.12 Hybotidae

Table B.23 Poisson distributed, generalised linear mixed model with log link for abundance of Hybotidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Hybotidae – Model 4				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-2.5863	0.7696	-3.361	P < 0.001
Forest type (NN)	0.5815	0.5300	1.097	0.273
Period (3)	3.5704	0.7054	5.061	P < 0.001
Year (2023)	1.0208	0.6770	1.508	0.132

Table B.24 AIC Results for Hybotidae. The best model is highlighted in bold.

Hybotidae - Model 4		
	df	AIC
Model 0	3	229.932
Model 1	10	203.243
Model 2	9	201.372
Model 3	8	200.041
Model 4	6	199.787
Model 5	7	201.787
Model 6	7	201.677

B.13 Sciaridae

Table B.25 Poisson distributed, generalised linear mixed model with log link for abundance of Sciaridae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Sciaridae – Model 3				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	5.9846	0.3770	15.873	P < 0.001
Forest type (NN)	-0.1849	0.2649	-0.698	0.485
Period (3)	-1.6447	0.6472	-2.541	0.011
Year (2023)	-0.4198	0.4703	-0.893	0.372
Mean precipitation	0.4767	0.2126	2.243	0.025
Mean temperature	-0.4315	0.2916	-1.480	0.139

Table B.26 AIC Results for Sciaridae. The best model is highlighted in bold.

Sciaridae- Model 3		
	df	AIC
Model 0	3	657.935
Model 1	10	625.404
Model 2	9	625.107
Model 3	8	624.735
Model 4	6	628.440
Model 5	7	628.266
Model 6	7	626.907

B.14 Dolichopodidae

Table B.27 Poisson distributed, generalised linear mixed model with log link for abundance of Dolichopodidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Dolichopodidae – Model 3				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-0.9883	0.7210	-1.371	0.171
Forest type (NN)	-0.1718	0.3994	-0.430	0.667
Period (3)	1.5227	1.1014	1.383	0.160
Year (2023)	-1.4853	0.8570	-1.733	0.083.
Mean precipitation	-0.5953	0.3195	-1.863	0.062.
Mean temperature	0.8233	0.6257	1.316	0.188

Table B.28 AIC Results for Dolichopodidae. The best model is highlighted in bold.

Dolichopodidae - Model 3		
	df	AIC
Model 0	3	168.119
Model 1	10	153.657
Model 2	9	154.090
Model 3	8	152.968
Model 4	6	154.868
Model 5	7	155.428
Model 6	7	155.530

B.15 Mycetophilidae

Table B.29 Poisson distributed, generalised linear mixed model with log link for abundance of Mycetophilidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Mycetophilidae – Model 0				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	1.7118	0.1862	9.195	P < 0.001

Mycetophilidae - Model 0		
	df	AIC
Model 0	3	317.772
Model 1	10	323.321
Model 2	9	322.488
Model 3	8	325.262
Model 4	6	322.299
Model 5	7	319.922
Model 6	7	320.156

Table B.30 AIC Results for Mycetophilidae. The best model is highlighted in bold.

B.16 Chironomidae

Table B.31 Poisson distributed, generalised linear mixed model with log link for abundance of Chironomidae.

 Site was used as a random effect together with an observation-level random effect (OLRE) to account for

 variation not explained by the predictors. Statistically significant values are marked in bold. Additional details

 on the predictors are found in Appendix A, Table A.3.

Chironomidae – Model 0				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-2.378	1.068	-2.227	0.026

Chironomidae - Model 0		
	df	AIC
Model 0	3	143.946
Model 1	10	153.953
Model 2	9	151.963
Model 3	8	151.656
Model 4	6	149.688
Model 5	7	151.139
Model 6	7	148.778

Table B.32 AIC Results for Chironomidae. The best model is highlighted in bold.

B.17 Syrphidae

Table B.33 Poisson distributed, generalised linear mixed model with log link for abundance of Syrphidae. Site was used as a random effect together with an observation-level random effect (OLRE) to account for variation not explained by the predictors. Statistically significant values are marked in bold. Additional details on the predictors are found in Appendix A, Table A.3.

Syrphidae – Model 0				
	Estimate	SE	z-value	<i>p</i> -value
Intercept	-0.2856	0.2739	-1.043	0.297

Syrphidae - Model 0		
	df	AIC
Model 0	3	160.277
Model 1	10	165.155
Model 2	9	164.723
Model 3	8	163.001
Model 4	6	161.848
Model 5	7	163.226
Model 6	7	162.903

Table B.34 AIC Results for Chironomidae. The best model is highlighted in bold.

Appendix C – Additional Results



C1. Diptera connectivity

Figure C.1 Abundance of Total Diptera and their correlation with connectivity. The Y-axis displays the abundance, and the X-axis represents the total volume of spruce trees within the specified radius around the sites. Connectivity is measured in (m^3) . The trendline indicates a correlation with connectivity for all three families.

C2. Phoridae temperature



Figure C.2 Abundance of Phoridae and the correlation with temperature. The Y-axis displays the abundance, and the X-axis represents the temperature (°C). The trendline indicates a correlation with temperature.



C3. Sciaridae precipitation

Figure C.3 Abundance of Sciaridae and the correlation with precipitation. The Y-axis displays the abundance, and the X-axis represents the precipitation (mm/day). The trendline indicates a correlation with temperature.



C4. Dolichopodidae precipitation

Figure C.4 Abundance of Dolichopodidae and the correlation with precipitation. The Y-axis displays the abundance, and the X-axis represents the precipitation (mm/day). The trendline indicates a correlation with temperature.

C5. Tachinidae precipitation

Table C.5 Tachinidae precipitation.



Figure C.5 Abundance of Tachinidae and the correlation with precipitation. The Y-axis displays the abundance, and the X-axis represents the precipitation (mm/day). The trendline indicates a correlation with temperature.



C6. Tachinidae temperature

Figure C.6 Abundance of Tachinidae and the correlation with temperature. The Y-axis displays the abundance, and the X-axis represents the temperature (°C). The trendline indicates a correlation with temperature.



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