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Insect Community Response to Recent Rewetting of Drained Bogs in Southeastern Norway

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Natural Resource Management

Preface

This study wraps up my master's degree in Nature Resource Managements and five memorable and educational years at the Norwegian University of Life Science (NMBU). It is one of four theses written as a part of a master's project announced by the Norwegian Nature Inspectorate (SNO), which surveys different effects of bog rewetting in Norway.

First and foremost, a big thank you to my main supervisor Jan Vermaat and two co-supervisors Jonathan E. Colman and Marte Fandrem for all guidance, support, and motivation during fieldwork, statistics, and writing. You made this master experience great, and I am very grateful for all the assistance along the way.

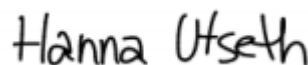
I also want to thank my three fellow students Aase Johansen, Eirik Walle and Ola Eian for the collaboration and for making intense field days memorable and fun. Our discussions and teamwork have boosted both my experience writing a thesis and the final result.

In addition, a big thank you to Norwegian Environment Agency for funding the field work and project, and to Pål Martin Eid (SNO) for first-hand knowledge about Norwegian rewetting, guidance in choosing bogs to include in the study, and for demonstrating mire rewetting in practice. I also want to thank Tone Birkemoe for the helpful suggestions and input to the implementation and execution of my field work.

To my roomies and friends at NMBU, thank you for making these past five years unforgettable and especially for making the past year a good "one of a kind" despite Covid-19 and the stress related to writing a master's. Finally, I also want to thank my family for the support and multiple pep-talks.

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Abstract

During the last five years, Norway has rewetted almost 80 drained mires to reduce climate emissions, limit the risk of natural disasters, and to prevent further loss of biodiversity. Even more mires are planned to be rewetted over the next five years despite limited knowledge on how mire fauna responds to the measures. Therefore, this study used insects to discover possible community alterations resulting from drainage and rewetting of ombrogenous mires, more commonly known as bogs, in the southeastern part of Norway. Changes in densities of insect orders and four target butterfly species were assessed through a transect study comparing seven newly rewetted bogs to adjacent and otherwise comparative drained and pristine areas. The findings revealed a general similarity in the overall composition of insect orders, butterflies, and water insects, despite some alterations within specific orders among the three treatments. Drained bogs generally had higher abundances of dipterans and hymenopterans compared to pristine areas, and lower abundances of orthopterans. These responses might derive from drainage favoring species preferring temporal water sources and forest development, rather than bog specialists. Insect communities in rewetted bogs were more similar to drained bogs than to pristine, with the exception of a reversing response in the order of hymenopterans. Additionally, rewetted bogs stood out in their high abundance of odonates, likely due to the increased access to artificial pools from dammed ditches. As the observations of target butterflies were few and the samplings were conducted shortly after rewetting, further assessments of lower taxa and long-term studies of responses are necessary to better understand the potential of bog rewetting for insect communities.

Sammendrag

I løpet av de siste fem årene har Norge restaurert nesten 80 drenerte myrer for å redusere klimagassutslipp, dempe risikoen for naturkatastrofer, og for å forhindre videre tap av biodiversitet. Enda flere myrer skal etter planen restaureres i løpet av de neste fem årene til tross for manglende kunnskap rundt hvordan myrfauna responderer på tiltakene. Denne studien brukte derfor insekter til å undersøke mulige endringer som følger av drenering og restaurering av ombrogene myrer, også kjent som nedbørsmyrer, i sørøstre del av Norge. Forandringer i tettheten til insektordre og fire sommerfuglarter ble derfor studert i en transektstudie som sammenlignet syv nylig restaurerte myrer til nærliggende og ellers sammenlignbare drenerte og uberørte myrer. Funnene avdekket en generell likhet i orden-, sommerfugl- og vanninsektsammensetning mellom behandlingene, til tross for noen forandringer innenfor spesifikke ordener. Drenerte myrer hadde generelt høyere forekomster av tovinger og vepser sammenlignet med uberørte områder, samtidig som de hadde lavere forekomster av rettvinger. Dette kan skyldes at drenering favoriserer arter som foretrekker midlertidige vannkilder og skog framfor mer myrspesialiserte arter. Videre lignet insektsamfunnet i restaurerte myrer mer på drenerte områder, med unntak av det som kan anses være en reverserende respons hos orden vepser. I tillegg skilte restaurerte myrer seg ut med mer øyenstikkere enn de to andre behandlingene, trolig på grunn av økt tilgang på åpne vann i kunstige dammer fra oppdemmede grøfter. På grunn av få observasjoner av de utvalgte sommerfuglartene, samt at undersøkelsene ble gjennomført kort tid etter restaurering, er det nødvendig med langtidsundersøkelser som inkluderer lavere taksonomiske nivåer for å kunne forstå potensialet til myrrestaurering for insektsamfunn.

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1 Introduction

Today, there is little doubt that human growth and exploitation of the planet Earth happen at the expense of nature, and alterations in land-use are often highlighted as one of the biggest threats towards the functioning of natural ecosystems (Foley et al., 2005). Wetlands, the ecosystems occurring where land and water unite, are classic examples of ecosystems vulnerable to human alteration (Van Asselen et al., 2013; Wetlands Internationals, n. d.). These ecosystems have commonly been, and still are, drained to improve agriculture or to facilitate forest production, affecting ecological processes and harming important habitats along the way (IUCN, 2017; Van Asselen et al., 2013). As a consequence, as much as 90% of the world's wetlands might have been lost since the beginning of the 17th century (Davidson, 2014; Ramsar Convention on Wetlands, 2018). Furthermore, around 20% of the almost 34 000 species living in connection with different types of inland wetlands are presently threatened by extinction according to the Red list of Threatened Species by the International Union for Conservation of Nature (IUCN, 2021).

Peatlands, a category within wetlands, are characterized by constant presence of water in the ground, creating waterlogged conditions and causing the decomposition of biological materials to halt (IUCN, 2017). As a result, partially decomposed plant materials build up and accumulate over time, slowly creating the characteristic peat substrate. After millennia, this slow accumulation of peat develops into natural carbon stocks (IUCN, 2017). Peatlands comprise both areas with ended and ongoing accumulation of peat, where the latter often is referred to as mires. Mires can be further defined into subgroups based on their water supply, where two main types are ombrogenous and geogenous mires (Joosten & Clarke, 2002). Ombrogenous mires, hereafter referred to as bogs, are fully dependent upon precipitation for both water and minerals. This makes them generally less nutritious than the geogenous mires, so-called fens, which get added nutrients and minerals from the soil (Joosten & Clarke, 2002; Wheeler & Proctor, 2000). In Norway, depending on the methods and definitions used in the calculations, between 9 and 14%, of the mainland is presently estimated to be covered by different kinds of peatlands, predominantly mires (Bryn et al., 2018; Rekdal et al., 2016; Tanneberger et al., 2017). Originally, mires covered larger parts of the country, but the last two centuries of large-scale drainage of mires have damaged a significant proportion of these areas (Joosten et al., 2015).

Drained mires have lowered water levels, which increases the decomposition of previously accumulated peat as the soil dries up and oxygen enters (e.g. Miljødirektoratet, 2021). Drainage

was previously a common measure to improve agriculture or forestry in Norway, but is presently prohibited by Norwegian regulations (Forskrift om nydyrking, 1997; Forskrift om berekraftig skogbruk, 2006). Nevertheless, centuries of degradation and loss of mires have resulted in several threatened mire types on the Red List for Ecosystems and Habitat types, and left over 300 peatland species on the Norwegian Red List for Species (Artsdatabanken, 2018; Henriksen & Hilmo, 2015). Enhanced knowledge about the value of pristine mires, both through ecosystem services and biodiversity, has increased the political urgency to preserve some of the remaining pristine areas. In addition to conservation, it has become progressively more common to actively try to reverse some of the damage already inflicted on mires and other types of wetlands through ecosystem restoration. The desired outcome of an ecosystem restoration process is generally to facilitate, and eventually achieve, similar ecosystem functions and characteristics as what otherwise would have existed had the degradation never occurred; i.e. the “pristine” state (SER, 2004).

Mire restoration has been recognized as an important measure against climate change and loss of biodiversity, and the first national plan for restoration of Norwegian wetlands was published in 2016 (Miljødirektoratet & Landbruksdirektoratet, 2016). The plan conveys objectives, experiences, implementation advice and cost estimates of restoration of different wetland types, including mires. Additionally, the plan states that the overall objectives of Norwegian wetland restoration are threefold: to counteract climate change, natural disasters and loss of biodiversity (Miljødirektoratet & Landbruksdirektoratet, 2016). To accomplish these objectives, about 17 million NOK of the National Budget for 2021 was reserved for the purpose of restoring drained mires in Norway (Prop. 1 S (2020–2021)). Additionally, the national plan was renewed in 2021 and proposed for five new years (Miljødirektoratet, 2021). In the meantime, between the first release and the renewed plan, about 80 Norwegian mires have been “rewetted” (Miljødirektoratet, 2021).

Multiple rewetting practices for different kinds of peatlands have been developed in recent years, and they all have the common goal to restore the original water level to prevent further erosion and dehydration of the land (Cris et al., 2014). Even though rewetting of mires has become an increasingly more common practice, there is a lack of knowledge whether rewetting works in restoring biodiversity and at what time scale this might occur. Moreover, published studies concerning the effects of rewetting on biodiversity indicate that the research focus has been weighted towards flora rather than fauna (Ruiz-Jaen & Aide, 2005; Watts & Mason, 2015; Wortley et al., 2013). Norway is no exception, and it is necessary to look for studies from other

Fennoscandian countries to find research regarding the effects of rewetting on fauna (Noreika et al., 2016; Punttila et al., 2016). The general perception seems to be that a successful restoration of vegetation is equivalent to a successful restoration of ecosystems, but this is often assumed rather than scientifically verified (Palmer et al., 1997). Even though vegetation might be fundamental in providing habitats and available niches for other species, the usage of solely vegetation to evaluate the success of a restoration process assumes the validity of the so-called Fields of Dreams hypothesis: “If you build it, they will come.” (Palmer et al., 1997). This hypothesis may not always reflect reality, as ecosystems are complex and specified by more than just bottom-up interactions (e.g. Estes et al., 2011; Hooper et al., 2005; Reitz & Trumble, 2002). This might be particularly relevant in an increasingly fragmented world with more isolated communities possibly affecting the re-colonization and distribution of species (e.g. Debinski & Holt, 2000; Thomas et al., 1992). Given the amount of time and money spent on each restoration project, it is important to establish whether the result is satisfactory and defending the effort made.

Although faunal surveys of restored mires are underrepresented, some studies have investigated the response of different kinds of birds and invertebrates to restoration measures (e.g. Alsila et al., 2021; Noreika et al., 2016; Punttila et al., 2016; Watts & Mason, 2015). Generally, insects have caught the attention of increasingly more people as their abundance is reported to be declining, possibly impacting the functionality of ecosystems and corresponding ecosystem services beneficial to all life on Earth (Hallmann et al., 2017; Losey & Vaughan, 2006; Sánchez-Bayo & Wyckhuys, 2019). This enthusiasm for insects is reflected in faunal studies of mire restoration as well, as mires hold a range of different microhabitats important to various insect species (e.g. Spitzer & Danks, 2006). Additionally, the degradation of different wetlands has contributed in making insects the most represented class of all threatened faunal species associated with wetlands on the Norwegian Red List for Species (Henriksen & Hilmo, 2015). Most studies including insects’ response to restoration and rewetting have focused on some selected target species or have been limited to include only a few orders (e.g. Noreika et al., 2016; Punttila et al., 2016; Taillefer & Wheeler, 2012). In other words, they usually investigate the reaction of a small portion of a much larger insect community. Nonetheless, these studies have revealed different and individual reactions to restoration among taxa and species (e.g. Noreika et al., 2016; Punttila et al., 2016; Taillefer & Wheeler, 2012).

To my knowledge, no Norwegian studies concerning insects’ response to drainage and rewetting of mires have yet been published. As described above, it is important to understand

the effects of mire rewetting on fauna. Especially since rewetting, regardless of the good intention of restoring natural ecosystems, is considered an anthropogenic disturbance of nature. Therefore, I investigated how the overall insect community responded to drainage and rewetting by comparing the abundances of different insect orders and target butterfly species in drained, rewetted and pristine bogs, in southeastern Norway. Additionally, ant nest mounds were counted alongside transects, and cotton-grass (genus *Eriophorum*) were inspected for the occurrence of targeted butterfly larvae. With these surveys, I aimed to reveal some of the variations and similarities in the insect composition and abundance among different treatments. My objective was to use these discoveries to evaluate whether current rewetting practices manage to reverse drainage inflicted changes in the short term of one to five years. The following two hypotheses were tested: (1) there is no difference in the insect community between pristine, rewetted and drained bogs, thus, rewetting has no effect on the insect community when compared to drained and pristine bogs, and (2) there is no difference in abundance of bog specialist butterflies between drained, rewetted and pristine bogs.

2 Materials and Methods

This thesis was a part of a master's project consisting of four different theses written by the master's students Aase Johansen, Eirik Walle and Ola Eian. The project assesses possible effects following drainage and rewetting of Norwegian bogs on vegetation, hydrology and insects. To compare patterns across studies and for logistical reasons, it was necessary and desirable to adapt fieldwork and study design within a cooperative context for all four studies.

2.1 Study design and area

Insect data were obtained from seven different locations in southeastern Norway, and included bogs in Oslo, Nes, Nittedal and Sandefjord municipalities in the counties of Viken, Oslo and Vestfold og Telemark (Figure 1, Table 1). Each location included one drained, one rewetted and one pristine bog, all mainly dependent on precipitation for water supply. In the selection of bogs to be included in the project, the Norwegian Nature Inspectorate (SNO) was helpful with information on rewetted bogs in Norway and which databases to use for bog-specific information (*Høydedata*, n. d.; *Myrrestaurering - innsynskart*, u. d.; *Naturbase*, 2020; *Norge i Bilder*, n. d.). All the rewetted bogs had been rewetted within the last five years, the earliest being in 2015 and latest in 2019 (Table 1). They were rewetted through the damming of ditches, where dams of bog material were created across the ditches to counteract the drainage of water

(Miljødirektoratet & Landbruksdirektoratet, 2016). In addition, other organic materials such as bushes and trees from the local area were used to partially plug the ditches between each of the dams. This was carried out with excavators, preferably of a particular type with wider tracks and when the bogs were frozen to minimize the damage. This is the presently established restoration method of bogs in Norway, primarily adapted from Finnish methodology (Miljødirektoratet & Landbruksdirektoratet, 2016).

It was not possible to use a full Before-After-Control-Impact (BACI) study design because of lacking data on the abundance of insects at the locations prior to drainage and rewetting. Instead, a matched pairing design was applied and insect densities at similar bogs of each treatment located as closely as possible to each other were compared. Four of the bogs, Sakkhusmåsan (L1), Aurstadmåsan (L3), Veggermyra (L8) and Skullerudmåsan (L11), were large enough to include multiple treatments within the same bog (Table 1).

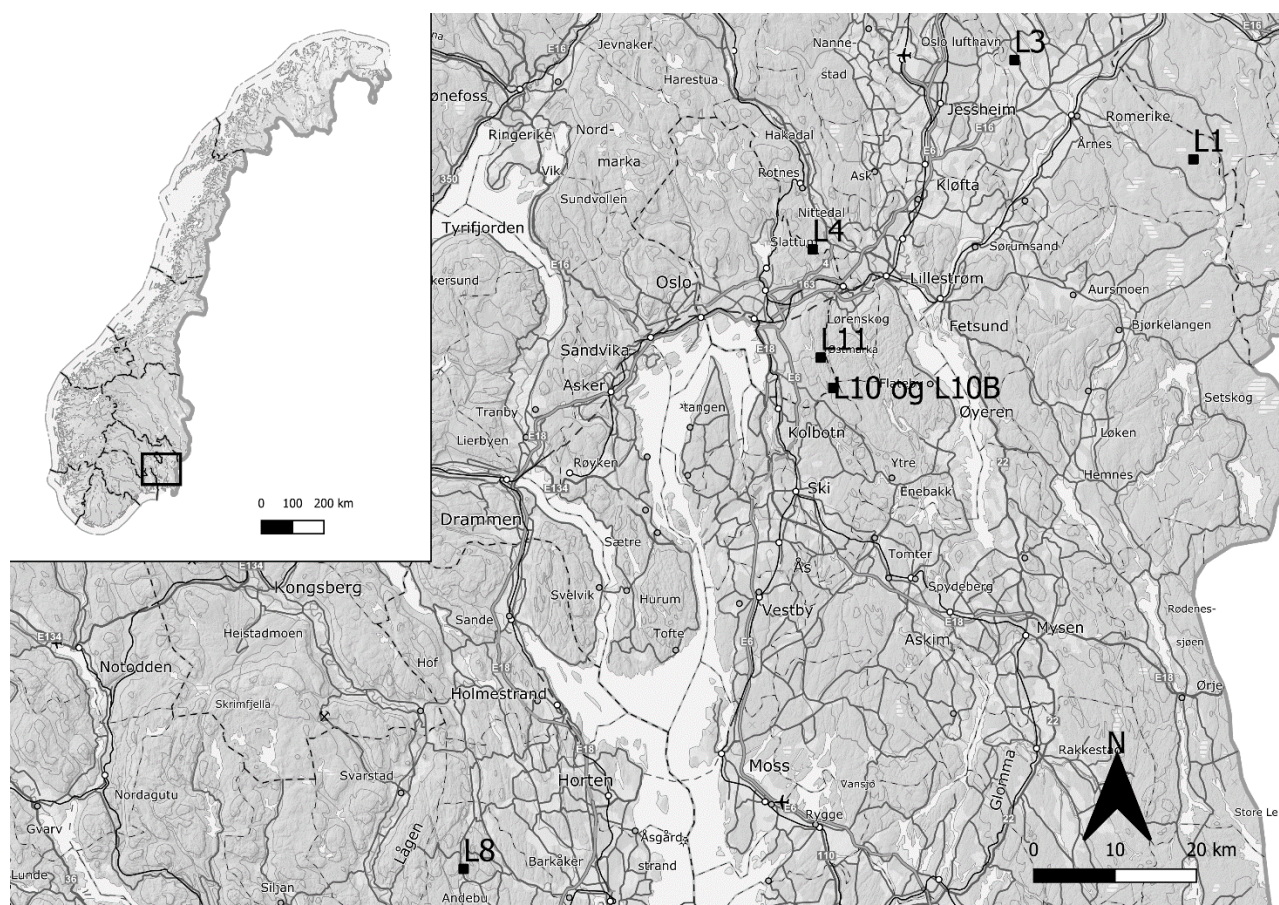


Figure 1: The seven study locations are found in southeastern Norway. Each location consists of one drained, one rewetted and one pristine bog area situated in two or three different bogs. L10 and L10B are located within the same area.

Table 1: Information about the study locations and bogs. Study bogs without names have been labeled “Untitled”. Four of the locations have bogs with multiple treatments, and the position of the treatments is marked with N (north), S (south), E (east) and W (west) in the bog name. The year of rewetting is written in parentheses under treatment. Two bogs were visited three times due to changes in the registration of insects. The star mark () behind dates implies visits with the first and incomplete registration method.*

Location	Bog	Treatment	Municipality	County	No. transects	Coordinates	1st visit	2nd visit	Re-visit
L1	Sakkuhsmåsan W	Pristine	Nes	Viken	2	60.071057, 11.729691	11.08.2020	20.08.2020	-
	Sakkuhsmåsan E	Rewetted (2015)	Nes	Viken	2	60.068417, 11.732275	11.08.2020	20.08.2020	-
	Villpostmyra	Drained	Nes	Viken	2	60.068616, 11.736222	11.08.2020	20.08.2020	-
L3	Aurstadmåsan W	Pristine	Nes	Viken	2	60.186776, 11.338898	12.06.2020	27.06.2020	-
	Aurstadmåsan E	Rewetted (2016)	Nes	Viken	3	60.183995, 11.344892	12.06.2020	28.06.2020	-
	Flakstadmåsan	Drained	Nes	Viken	2	60.171462, 11.331945	13.06.2020	29.06.2020	-
L4	Untitled	Pristine	Nittedal	Viken	2	60.002778, 10.866177	11.06.2020	19.06.2020	-
	Romsmåsan	Rewetted (2016)	Nittedal	Viken	3	59.984927, 10.884238	10.06.2020	19.06.2020	-
	Untitled	Drained	Nittedal	Viken	3	59.995520, 10.878745	11.06.2020	19.06.2020	-
L8	Veggermyra N	Pristine	Sandefjord	Vestfold og Telemark	2	59.312006, 10.094829	13.08.2020	25.08.2020	-
	Veggermyra S	Rewetted (2018)	Sandefjord	Vestfold og Telemark	2	59.310722, 10.095210	13.08.2020	25.08.2020	-
	Strandemyra	Drained	Sandefjord	Vestfold og Telemark	2	59.312039, 10.075883	13.08.2020	25.08.2020	-
L10	Untitled	Pristine	Oslo	Oslo	1	59.844256, 10.913112	02.06.20*	17.06.2020	09.06.2020
	Fjøsmåsan	Rewetted (2019)	Oslo	Oslo	2	59.831925, 10.921613	02.06.20*	16.06.2020	-
	Blåsynmåsan	Drained	Oslo	Oslo	3	59.846195, 10.943072	09.06.2020	17.06.2020	-
L10B	Stormyr	Pristine	Oslo	Oslo	2	59.820100, 10.928521	04.06.2020	17.06.2020	-
	Eriksvannmåsan	Rewetted (2019)	Oslo	Oslo	2	59.832767, 10.927913	03.06.20*	16.06.2020	04.06.2020
	Starmåsan	Drained	Oslo	Oslo	3	59.820552, 10.928648	04.06.2020	17.06.2020	-
L11	Skullerudmåsan S	Pristine	Oslo	Oslo	2	59.860812, 10.860107	13.06.2020	26.06.2020	-
	Ølgårdsmåsan	Rewetted (2019)	Oslo	Oslo	3	59.865111, 10.893789	14.06.2020	26.06.2020	-
	Skullerudmåsan W	Drained	Oslo	Oslo	2	59.861424, 10.859165	13.06.2020	26.06.2020	-

2.2 Study species

All insects observed during the transect walks were registered, mostly by families, superfamilies, suborders, or orders. In addition, four butterfly species were chosen as target species; Juttas Arctic (*Oeneis jutta*), Moorland Clouded Yellow (*Colias palaeno*), Cranberry Blue (*Agriades optilete*) and Large Heath (*Coenonympha tullia*). These butterflies prefer wetlands as feeding and breeding habitats, and are considered to be mire specialists (Noreika et al., 2016; Aarvik & Elven, 2014a; Aarvik & Elven, 2014b; Aarvik & Elven, 2014c; Aarvik & Elven, 2014d). In addition, they are species within the superfamily Papilionoidea and have specific characteristics that make them relatively easy to species determine during transects counts. Also, these species are relatively common species in the southeastern part of Norway, and are all categorized as “least concern (LC)” on the Norwegian Red List for Species (Henriksen & Hilmo, 2015). The flight period varies between the four species, and while *O. jutta* may be seen from early June to early July, the three other species usually have flight periods from mid-June to late July or the beginning of August (Aarvik & Elven, 2014a; Aarvik & Elven, 2014b; Aarvik & Elven, 2014c; Aarvik & Elven, 2014d). Even though they are considered to be mire specialists, some of the species do survive in drier areas and feed on flowers and plants outside mires (Noreika et al., 2016). Additionally, *A. optilete* has larvae living on plants not typically associated with mires or other wetlands (Aarvik & Elven, 2014b).

2.3 Field work

The field work was conducted during June and August of 2020. Due to the targeted butterfly species and other flying insects, it was necessary to sample during certain weather conditions to maximize the chance of observation. A combination of the monitoring criteria for United Kingdom Butterfly Monitoring Scheme (UKBMS) and the national monitoring of butterflies and bumblebees in Norway was used to develop environmental criteria for transect sampling (UKBMS, n. d. ; Öberg et al., 2011). As an outcome, counts were not conducted during rainfalls, temperatures below 15 °C, or when the wind forecast reported more than six meters per second. In addition, transect counts were only performed between 10:00 a.m. and 17:00 p.m. All line transects were walked twice, with at least one week in between each walk, except from the transects at the rewetted bog in L10B and the pristine bog in L10. These transects were walked three times during three different days as insects were registered exclusively within orders during the first visit. The registration method was later altered to include suborders, families, superfamilies and species, and most of the bogs with “incomplete” registrations were re-visited.

Due to time limitations, rewetted L10 was not re-visited and therefore include one “complete” and one “incomplete” registration of insects (Table 1).

Every location was represented by a drained, rewetted and pristine bog or area, and had between one to three line transects for each treatment. The transects ranged between 30 and 50 meters long. Some of the rewetted and drained bogs allowed for pristine areas within the same bog, and these bogs contributed with transects of different treatments (Table 1). In drained and rewetted bogs, transects always crossed perpendicular to one or more ditches or plugged ditches. If the bogs contained ponds, at a minimum one line transect was placed close to, or directly crossed, open water. When the weather conditions were met, registrations of insects within a belt of one meter on each side of the transect line were carried out with a pace of 0.15 minutes (9 seconds) per square meter. Transect counts only included insects within a limited height above the ground (roughly two meters). In addition, only members of the class Insecta were recorded, and individuals from other subphyla or classes of arthropods were ignored during the transect counts. All insects were at least registered within orders or as unknown insects. Some of the more characteristic insects were recorded at lower taxonomical levels, such as within suborders, superfamilies, families or as specific species.

Besides insects, ant nest mounds were counted within two meters on each side of the transect line. These counts were made to discover differences between the number of mounds between treatments as a sign of changed environmental conditions. Additionally, 20 cotton-grass clusters (genus *Eriophorum*) outside the transect belts were examined for larvae of the targeted butterfly species. Both these counts could be conducted regardless of the weather or time of the day. On large bogs with multiple treatments, 20 cotton-grass clusters were inspected within each treatment.

2.4 Data analysis

The dataset used in the data analysis included samplings from all transects and visits, in addition to counts of ant nest mounds around transects and larvae on cotton grass. RStudio was applied in all the statistical analysis (RStudio Team, 2020). In addition, the ggplot command from the tidyverse package was used to visualize the data (Wickham, 2016). Generalized linear mixed models (GLMM) and the glmmTMB command from the glmmTMB package were used to analyze the effects of drainage and rewetting on the insect community (Brooks et al., 2017; RStudio Team, 2020). Counts with enough registrations (10 or more) worked as response variables following a Conway-Maxwell Poisson error distribution to account for somewhat

underdispersed data. All insect orders were tested with treatment as a fixed effect and transects nested within bogs further nested within locations as a random effect. Parts of the nesting, either bog or location, were removed for some of the orders. This was to improve and individualize the fit of the model and to prevent over-parametrization. Additionally, visit dates were converted to Julian dates and treated as a random partially crossed effect. To account for varying transect lengths, an offset with transect length was included in the models.

In addition, non-metric multidimensional scaling (NMDS) with the Vegan package was used to compare different parts of the insect communities in drained, rewetted and pristine bogs (Oksanen et al., 2020). The first NMDS was of the orders composition, where insect orders per square meter for each treatment in every location were compared. Secondly, NMDS was used to compare specialist butterflies and the butterfly communities among treatments. Finally, insects associated with water were collectively compared among treatments. Taxa of insects with parts of or their entire life history in water were included, like the families Gerridae and Culicidae, suborders Anisoptera and Zygoptera, as well as the order Trichoptera and other unknown water beetles. In this analysis, the first visit for the rewetted and pristine bogs at L10 (Fjøsmaßen) and rewetted bog at L10B (Eriksvannmosan) were excluded due to lack of registrations of lower taxa. Additionally, visits with zero observation in any of the taxa were excluded, and Bray-Curtis dissimilarity calculation was used for all the NMDSs. In addition, to look at the variance between communities of different treatments, Adonis was used as a permutational analysis (Oksanen et al., 2020).

3 Results

A total of 4399 insects were registered and classified into 10 different orders. Diptera and Hymenoptera were the two most abundant orders for all treatments (Figure 2), despite large variation among locations and treatments (see Figure A1). In addition, about 12% of the insects were not identified and grouped as unknown. Seven orders had enough data to be further tested with GLMM. The three orders excluded from GLMM were Blattodea, Trichoptera and Neuroptera, each with less than seven registrations. Only eight ant mounds were counted alongside the transects, which were too few to be able to further test for significance between treatments (see Figure A2). No larvae were observed on cotton gras.

Additionally, none of the four specialized butterfly species had enough registrations to be analyzed individually with GLMM or ordination. Consequently, these were analyzed together

with the rest of the lepidopterans. The number of registrations varied between species. *O. jutta* was not sampled at all, while *C. tullia* was the specialist species most often observed, even though this species had only four registrations in total (see Figure A3).

3.1 Differences in abundances following drainage

In total, most insects per square meter were registered in drained bogs, with Diptera, Hymenoptera and Hemiptera being the most abundant orders (Figure 2). In general, the abundances of three orders, Diptera, Hymenoptera and Orthoptera, were significantly different between drained and pristine bogs (Table 2, Figure 3D, 3F and 3J). Drained bogs had significantly higher abundance of dipterans and hymenopterans, while they had a lower number of orthopterans per square meter than pristine bogs (Table 2, Figure 3D, 3F and 3J).

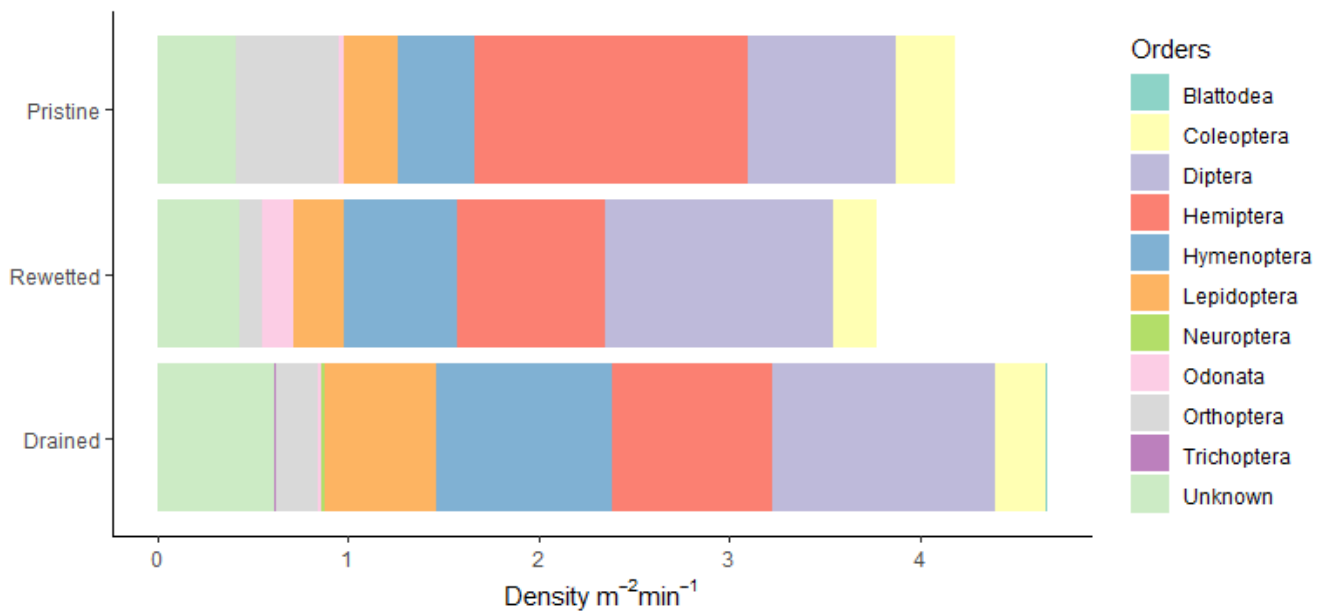


Figure 2: The average contribution of each insect order to the average density of insects (square meter per minute) observed within drained, rewetted and pristine bogs.

Table 2: Generalized Linear Mixed Model (GLMM) summaries of the models slope estimates (Est.), standard errors (SE) and p-values for all orders with more than 10 observations and for the total number of insects. Bold fonts represent significant p-values, and star marks indicate the degree of significance (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$). Drained-pristine and drained-rewetted was compared with drained treatment as intercept. The comparisons of pristine-rewetted had pristine as intercept. Blattodea, Trichoptera and Neuroptera are not included due to few registrations.

ORDERS		DRAINED - PRISTINE	DRAINED - REWETTED	PRISTINE - REWETTED
Total	Est.	-0.126	-0.105	0.021
	SE	0.126	0.124	0.118
	<i>p</i>	0.319	0.399	0.860
Coleoptera	Est.	0.374	0.423	0.049
	SE	0.246	0.299	0.289
	<i>p</i>	0.129	0.157	0.866
Diptera	Est.	-0.447	-0.023	0.425
	SE	0.189	0.180	0.183
	<i>p</i>	0.018 (*)	0.900	0.020 (*)
Hemiptera	Est.	0.244	0.216	-0.028
	SE	0.426	0.444	0.350
	<i>p</i>	0.567	0.627	0.936
Hymenoptera	Est.	-0.885	-0.385	0.501
	SE	0.375	0.357	0.342
	<i>p</i>	0.018 (*)	0.281	0.143
Lepidoptera	Est.	-0.431	-0.264	0.167
	SE	0.306	0.305	0.296
	<i>p</i>	0.158	0.386	0.572
Odonata	Est.	0.104	2.989	2.579
	SE	0.911	0.748	0.803
	<i>p</i>	0.909	< 0.001 (***)	0.001 (**)
Orthoptera	Est.	1.252	-0.541	-1.793
	SE	0.442	0.440	0.428
	<i>p</i>	0.005(**)	0.2187	< 0.001 (***)

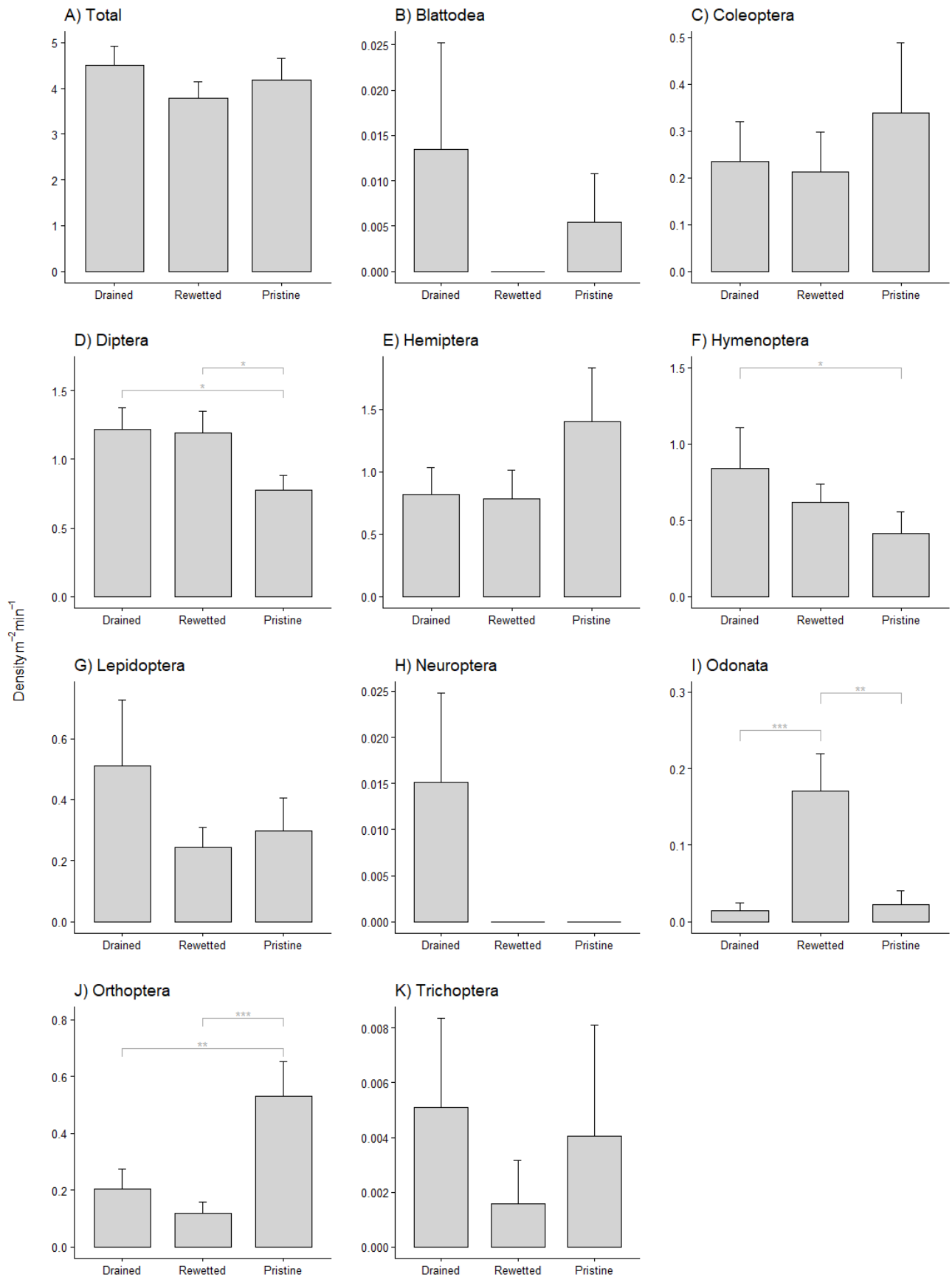


Figure 3: Densities of total insects and of each insect order. The y-axis is showing the average number of insects recorded per square meter per minute. Note that the scaling of the y-axis varies between plots. Bars illustrate the mean value for bogs of each treatment, and error bars represent upward standard errors (SE). Star marks represent significant codes from the GLMMs (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$).

3.2 Differences in abundance following rewetting

The lowest registered density of insects per square meter per minute was found at rewetted bogs (Figure 2). Rewetted bogs differed significantly from pristine bogs for the three orders Diptera, Odonata and Orthoptera. There were significantly more dipterans and odonates in rewetted bogs, but less orthopterans compared to pristine (Table 2, Figure 3D, 3I and 3J). Additionally, rewetted bogs differed from drained bogs through the abundance of Odonata, which was generally higher in rewetted bogs (Table 2, Figure 3I).

3.3 Community similarities among treatments

There was no significant difference for the general insect community (Treatment, $R^2 = 0.14$, $p = 0.18$), the lepidopteran community (Treatment, $R^2 = 0.05$, $p = 0.85$), or the assemblage of insects associated with water (Treatment, $R^2 = 0.16$, $p = 0.33$) between drained, rewetted and pristine bogs (Figure 4, 5 and 6).

The total abundance of insects between the three treatments also overlapped, and the three orders Coleoptera, Hemiptera and Lepidoptera were not significantly different in abundance for any of the comparisons (Table 2, Figure 3C, 3E and 3G). For drained and rewetted bogs, the abundance of order Odonata was the only order significantly dividing these two treatments from each other (Table 2, Figure 3I).

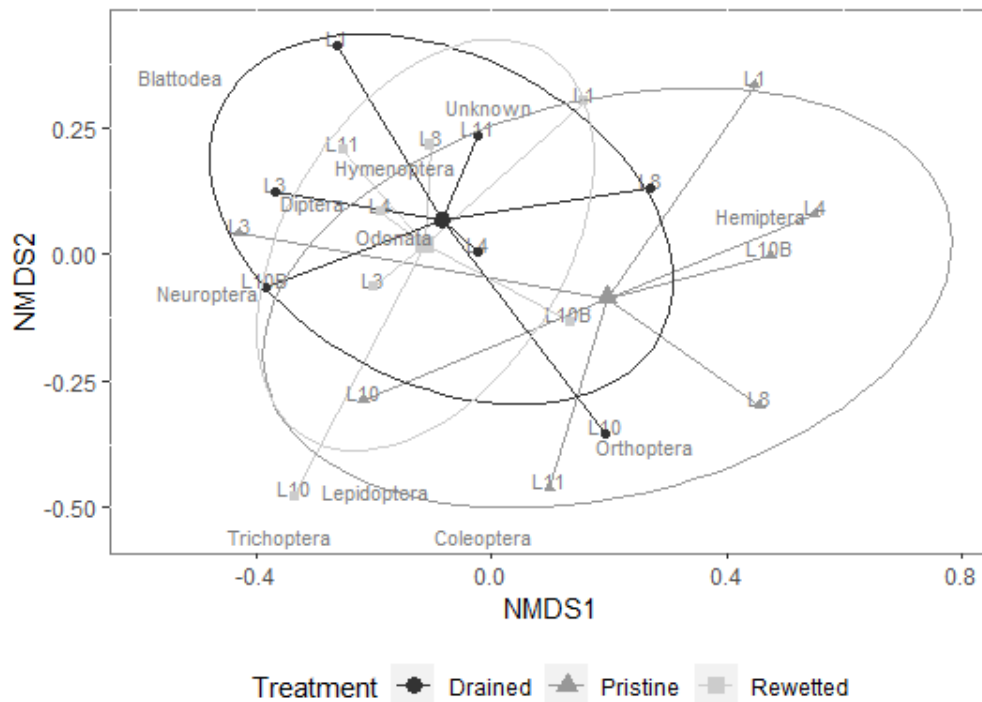


Figure 4: A two dimensional NMDS of the order assemblage in drained, rewetted and pristine bogs. The ellipses represent 1 standard deviation (SD) and spider webs connect and draw the centroids for each of the three treatments in every location. None of the treatments were significantly different from one another.

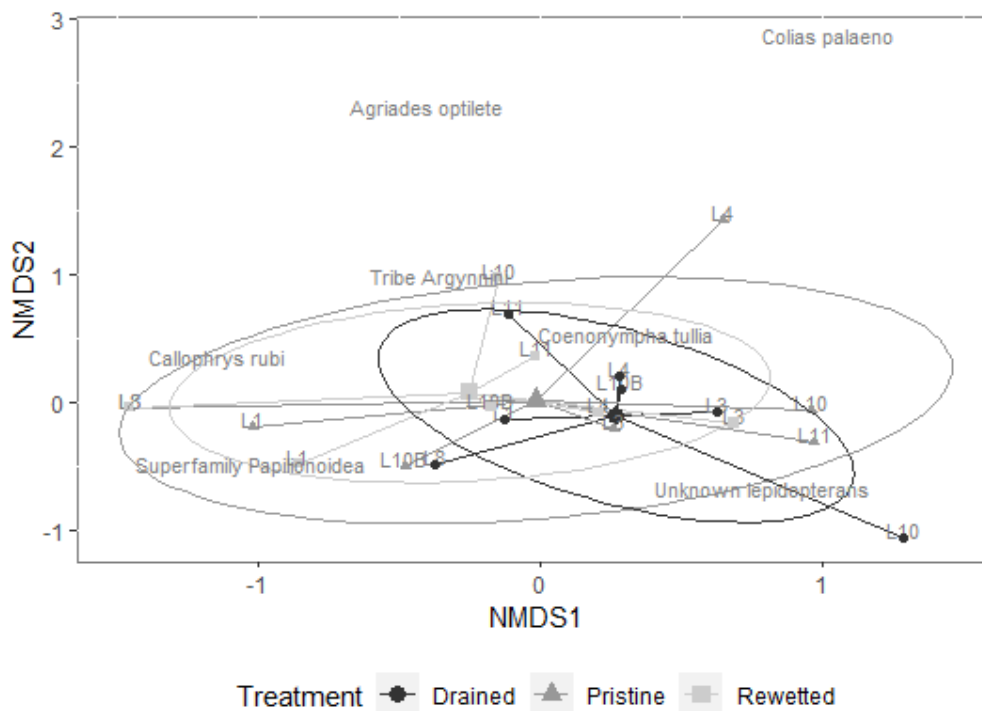


Figure 5: A two dimensional NMDS of the butterfly community in drained, rewetted and pristine bogs. The ellipses represent 1 SD and spider webs connect and draw the centroids for each of the three treatments in every location. None of the treatments were significantly different from one another.

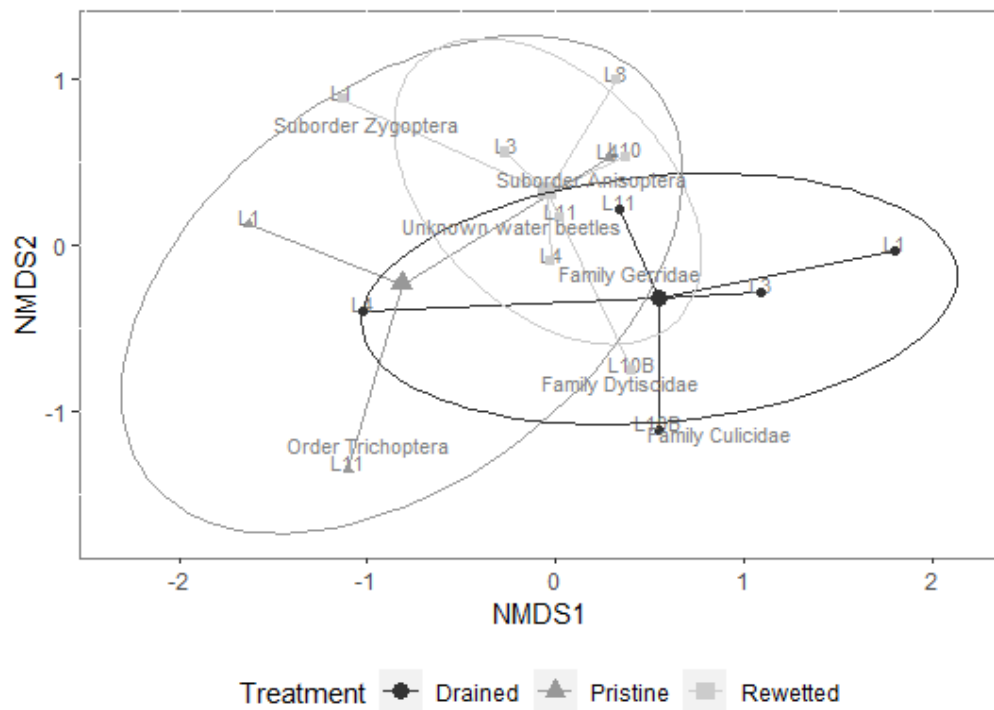


Figure 6: A two dimensional NMDS of orders, suborders and families fully or partly associated with water in drained, rewetted and pristine bogs. The ellipses represent 1 SD and spider webs connect and draw the centroids for each of the three treatments in every location. None of the treatments were significantly different from one another. Note that pristine bogs at location L3, L8, L10 and L10B, and drained bogs at location L8 and L10 were excluded due to zero observation of the included taxa.

4 Discussion

Despite similarities in the composition of orders, butterflies and water insects among drained, rewetted and pristine bogs, the treatments seem to influence the insect community by adjusting the abundances of some individual orders. Even though the differences were order specific, it indicates that drainage has the potential to cause long lasting and persistent changes in communities. Furthermore, the findings implied that rewetting is unable to counteract drainage inflicted alteration within the first five years for most orders. Unfortunately, without transect counts prior to drainage, it is impossible to know the true abundances of each insect order in pristine bogs within the region, or even country, studied here. Also, without species information one can only speculate based on other similar studies about what ways drained and rewetted communities differ from pristine. The variations may be due to altered species abundances, changes in species richness, or a combination of the two. Due to inadequate and limited registrations of the targeted butterfly species and ant nest mounds, it was impossible to evaluate how the different treatments impacted their presence. This calls for further studies of species response to rewetting of Norwegian bogs at a larger spatial scale and possibly in landscapes where recolonization with such species is likely. Importantly, this also emphasizes the need for a better understanding and communication of the timespan necessary for bog restoration processes.

4.1 Persistent changes despite rewetting measures

Three orders indicated changes following drainage: Diptera, Orthoptera and Hymenoptera. Additionally, the abundance of Diptera and Orthoptera in drained bogs were indistinguishable from those in rewetted bogs, implying that the rewetting measures had not counteracted the changes within one to five years.

Dipterans were generally more abundant in rewetted and drained bogs, which often include open or plugged ditches filled with water. This access to open water might be beneficial for dipterans with a larval stage depending on water to complete their life cycle (Schäfer et al., 2006). Additionally, species within the dipteran family Culicidae, more commonly known as mosquitos, have previously been found to prefer habitats with tree cover and temporary ponds (Schäfer et al., 2006). Since drainage usually facilitates forest growth and alters the availability of permanent bog pools, it might also improve the habitat suitability for mosquitos in bogs (e.g. Elo et al., 2015; Jukaine et al., 1995). In addition, a study by Taillefer and Wheeler (2012) assessed the response of species within the suborder Brachycera in restored bog patches

previously used as peat mines. They found the community structure and species diversity in drained areas to differ from that of both pristine and restored areas seven years after restoration measures were completed, despite similarities in the overall species composition. In general, disturbed bogs had some few dominating species accounting for larger parts of the total abundance, in contrast to the two other treatments with less dominance of individual species (Taillefer & Wheeler, 2012). Therefore, contrary to my findings, their results indicated some reversal of drainage inflicted change and suggested alterations towards a more pristine-like dipteran community. If this applies to other dipteran species as well, more time may be needed before the same reversing trends occur in the rewetted bogs included in this study. However, like Taillefer and Wheeler (2012) also highlighted, one should bear in mind that each ecosystem is unique, and therefore the response of species might differ between areas due to different prerequisites.

Unlike dipterans, orthopterans existed in higher abundances in pristine bogs compared to both drained and rewetted bogs. There are few existing publications concerning orthopterans and mire restoration, which makes it difficult to interpret the underlying reasons for the differences in abundance between treatments. However, orthopterans are hemimetabolic insects and for most species neither adults nor juveniles are dependent upon open water to complete their life cycle. However, Norway has some species associated with bogs and other types of mires, like *Metrioptera brachyptera* (see Figure A4) and *Pseudochorthippus montanus* among others. These species are described to have narrow niches, requiring specific moist or wet habitats and conditions to be able to survive and reproduce. Additionally, they are considered to have limited dispersal abilities due to reduced wings (Poniatowski & Fartmann, 2010; Weyer et al., 2012). Consequently, species like these might struggle to survive in altered conditions following drainage, as well as struggle to recolonize restored areas even if rewetting manage to reestablish suitable conditions. This may contribute to persistently lower abundances of orthopterans following drainage despite completed rewetting measures.

Generally, the distance between pristine and rewetted bogs might be of great importance for the recolonization of species of multiple orders. Pristine bogs are often considered to be scattered “islands” working as important refuges for specialized species (Spitzer & Danks, 2006). The comprehensive, almost full scale, and complete drainage of Norwegian mires over the last centuries might have contributed to further isolate and reduce the availability of these patches. Studies have indicated that distance plays an important role in the restoration of communities (e.g. Watts & Mason, 2015), and a study from a peat mine in New Zealand found the

recolonization of beetles in restored patches to vary with distance and time (Watts & Mason, 2015). Generally, the longer the distance to pristine areas and the shorter the time since restoration, between 2-13 years, the bigger the difference in beetle abundance and richness between restored and pristine patches (Watts & Mason, 2015). This was explained by some of the species' poor ability to disperse and recolonize. In another study, the short distance between rewetted and pristine bogs was highlighted as crucial for the rapid reestablishment of many of the targeted species (Noreika et al., 2015). Based on these studies, one might argue that the extensive drainage of bogs throughout Norway has caused further isolation of bog habitats, and thereby reduced the restoration success in terms of insect establishment. If this is the case, the rewetted bogs included in this study might have been too challenging to reach and colonize within the short time span since restoration. In addition, rewetted bogs with pristine areas might experience a more rapid recolonization of specialist species. Three study locations, L1, L3 and L8, included pristine and rewetted areas within the same bog, and within these bogs the abundance of dipterans showed signs of reversing response towards a more pristine-like community (see Figure A5). However, orthopterans did not respond in a similar manner, and further investigations are necessary to understand the importance of pristine areas in the immediate vicinity to rewetted bogs (see Figure A6).

In addition to distance, short time span between rewetting and monitoring might be a likely reason behind few reversing effects following rewetting. The rewetted bogs had been rewetted within five years prior to samplings, and most of them within the last two years. Additional time may be necessary before it is possible to observe greater changes towards more pristine abundances in these orders. Studies concerning the effects of restoration practices on faunal reestablishment support the importance of time in restoration projects and have recorded improvements in insect biodiversity and abundances over time (e.g. Watts & Mason, 2015). However, most studies do not observe complete reestablishment of all specialist species, despite rather rapid recovery of some species within the first five years (e.g. Elo et al., 2015; Mazerolle et al., 2006; Noreika et al., 2015). Some long-term studies have even reported unsuccessful reestablishment of characteristic bog species up to nearly two decades after restoration measures were conducted (e.g. Strobl et al., 2020). This persistent absence of some species several decades after rewetting measures have been completed challenge the validity of the Field of Dream hypothesis (e.g. Noreika et al., 2015; Noreika et al., 2016; Watts & Mason, 2015).

4.2 Changes of insect orders and communities following rewetting

Due to the general registration of insects within orders, most of the differences we can expect to see between treatments are variations in the abundances of orders associated with specific conditions. Rewetting aims to increase the water level and might therefore reestablish refuges and niches for species especially adapted to moist conditions or open waters. In this study, Odonata and Hymenoptera were the only two orders with observed alterations in abundances following rewetting.

Odonates, with dragonflies and damselflies, have in previous studies been used as bioindicators for changes in habitats and conditions of wetlands (e.g. Elo et al., 2015; Krieger et al., 2019; Strobl et al., 2020). In these studies, drainage generally reduces both the abundance and diversity of dragonflies and damselflies, possibly due to changes in suitable habitats, breeding sites and food supply to their aquatic juvenile stages (e.g. Elo et al., 2015; Remm & Sushko, 2018). Additionally, Odonata is one of few taxa previously monitored following bog rewetting in Norway, and species in dammed pools and natural pools have been registered and presented in a note to the County General in Møre og Romsdal. This note points out that artificial bogs have a rich Odonata diversity, and that they possibly even have increased their species richness since rewetting (Dolmen, 2020). However, no statistical analyses seem to have been presented from the monitoring to this date. From other studies, restoration measures appear to be able to bring back the total number of odonate species and abundances equal to that of pristine mires, despite varying species compositions between the treatments (Krieger et al., 2019; Remm & Sushko, 2018).

In this study, the odonate abundance in pristine bogs resembled that of drained ones, while they were the most abundant in rewetted bogs. One explanation behind higher abundances in rewetted sites might be the increased access to open water and ponds due to dammed ditches (Eian, 2021). Since odonates have a larval stage generally dependent upon water, these dams might increase the availability of suitable larval habitats for some species (Beadle et al., 2015; Strobl et al., 2020). Even though drained bogs also can contain some ditches filled with water, these shallow and narrow pools might not be suitable habitats for all species (Elo et al., 2015). Another explanation can be that the study design itself has affected the number of odonates recorded for the different treatments. Transects in rewetted bogs always crossed a minimum of one ditch perpendicularly. In pristine bogs with open waters, the transect were usually located next to the ponds due to unsafe ground surrounding the water. This have impacted how close and frequently transect counts were to open water and may also have influenced the results if

some species of odonates prefer to stay closer to water. However, an American study of adult dragonflies' land use around open water found unaffected abundances of dragonflies up to 160 meters from the closest pond (Bried & Ervin, 2006), suggesting that at least several dragonflies should not be notably affected by transects crossing by or directly over open waters.

The order of Hymenoptera was the only order where rewetted bogs in general had an intermediate abundance between pristine and drained bogs. Based on hymenopterans, it appears like bog rewetting is an appropriate measure to reestablishing natural and pristine communities in drained bogs, but it is still uncertain whether it manages to restore the species composition as well as abundance. One of few published studies concerning hymenopterans and mire restoration revealed varying responses among several ant species within the three first years since restoration (Punttila et al., 2016). Drained mires were the most species rich due to the coexistence of forest and mire ants, even though they in general had fewer mire specialist species compared to pristine mires. However, rewetting appeared to counteract some of the assemblage changes, and managed to decrease the presence of the species associated with forests (Punttila et al., 2016). Even though the abundances of hymenopterans show promising and rapid effects from rewetting measures in this study, one should notice that this order was the exception rather than the rule. For other orders, rewetting seem to have failed to fully reestablish pristine communities prior to the study.

4.3 Similarities between pristine, drained and rewetted bogs

Three of the orders, Lepidoptera, Hemiptera and Coleoptera, did not differ in abundance between the three treatments. In theory, it is possible that none of these orders are affected by the treatments, but in the light of similar studies this seems rather unlikely (e.g. Noreika et al., 2016; Strobl et al., 2020; Watts et al., 2008; Watts & Mason, 2015).

To my knowledge, previous studies have only partly investigated aquatic hemipteran's response to drainage (Beadle et al., 2015; Mazerolle et al., 2006), however, there are some studies assessing the response of beetles and butterflies (e.g. Noreika et al., 2016; Strobl et al., 2020; Watts et al., 2008; Watts & Mason, 2015). In contrast to the findings of this study, studies of beetle communities have previously discovered differences between restored and pristine mire patches within six years since restoration, with the most individuals and species being found in pristine areas (Watts et al., 2008; Watts & Mason, 2015). Additionally, the same two studies indicated improved restoration of pristine beetle communities over time, and both abundances and species richness reflected that of pristine areas after nine years (Watts et al., 2008; Watts &

Mason, 2015). Unlike this study, they assessed beetles in a mined bog where restored treatments were patches within the same bog as pristine treatment. Thus, the beetles could have migrated to more suitable patches nearby when the disturbance first occurred, and then traveled back after restoration. In more isolated bogs, like the majority of the bogs included in this study, the long distance between suitable habitats might have forced most beetles to stay and make the best of a bad situation when drainage first occurred. Hence the similarities between all treatments. On the other hand, numerous studies support the replacement of specialist species with generalists following drainage (e.g. Noreika et al., 2016; Punttila et al., 2016). Therefore, it seems rather doubtful that all species have survived and managed to adapt to drainage, even though these findings do not show any differences between treatments.

The included target butterfly species were supposed to increase the understanding of the potential effects of drainage and rewetting on individual specialist species. Due to the combination of short flight periods and limited available field days, several transect counts were conducted outside normal flight periods which likely contributed to few observations. The comparison of the butterfly composition, including the target species, resulted in no significant difference between treatments. However, previous studies of butterflies have resulted in divergent findings (Noreika et al., 2016; Strobl et al., 2020). A survey by Noreika et al. (2016) assessed some of the same butterfly species included as target species in this study, and their discoveries implied varying butterfly communities among pristine, drained and restored mires. Furthermore, drained mires were overall more dominated by generalists, and had relatively low abundances of specialist butterflies. They also discovered an increase in the abundance of specialist butterflies following restoration, even though this increase did not apply to all species (Noreika et al., 2016). In contrast, a newly published study by Strobl et al. (2020) did not see the same positive results, and reported that specialized species were still missing 20 years after restoration measures were completed. They highlighted the lack of nearby source populations due to fragmentation as a possible reason for the contrasting outcome, supporting the value of distance between pristine and rewetted areas for successful re-establishment of specialist species.

The ordination plot of water insect composition did not imply any differences between drained, rewetted and pristine bog areas. However, the plot should be interpreted with some caution due to the low number of pristine bogs able to be included in the NMDS because of missing observation within any of the included water taxa. On the other hand, this might suggest a variable availability of suitable habitats for water insects in pristine bogs compared to newly

rewetted areas. All rewetted bogs had registration within at least one of the water taxa and could be included in the analysis, proposing a more general availability of pools and open waters. This might derive from the artificial flooded pools that occur shortly after the plugging of ditches providing habitats for water species (Eian, 2021). Other surveys have indicated that artificial bog pools have the ability to provide habitats for many of the same species as natural pools (Hannigan et al., 2011). However, the limited data on taxa in natural and artificial pools prevent a strong test of the assumption of increased access of suitable habitats for water species following rewetting, and needs to be further studied.

The presently used order-based approach to assess the insect community, revealed similarities in the overall insect composition and abundance of orders among treatments. Hence, one may ask whether an assessment of orders is an adequate resolution to discover effects on insect communities following bog rewetting. To sample higher taxa instead of species is a more resource efficient approach to assess bigger aspects of insect communities with limited time and resources (e.g. Bates et al., 2007). However, the usage of orders can only provide a general picture of the insect community and which orders are dominating or absent, while intricate variations between treatments are most likely not included without more detailed registrations of lower taxa. Hence, the communities might appear more similar than they really are. The best suited sampling resolution considering both resource use and ecological precision for biodiversity monitoring has been discussed in numerous papers (e.g. Bates et al., 2007; Rosser, 2017). Since the assessment and identification of all species in an ecosystem is relatively resource demanding, it is widespread to compromise the sampling to only a few indicator species or some selected higher taxa when investigating developments and changes in ecosystems (e.g. Noreika et al., 2016; Punttila et al., 2016; Taillefer & Wheeler, 2012). Some scientists are even questioning the necessity of a comprehensive assessment of all species in restoration studies, as they see a complete restoration of species assembly as a rather unrealistic ambition (Palmer et al., 1997). They consider it to be more beneficial to concentrate on restoring the functionality and structure of communities, and therefore focus the monitoring towards functional groups or species with large impacts on pristine ecosystems (Palmer et al., 1997). These species are typically referred to as keystone species, and might be of great importance for the restoration of disturbed ecosystems (Mills et al., 1993). In addition, assessing families or genus have shown promising results in other ecosystems (Bates et al., 2007), and might be a more suitable resolution for assessments of mire communities as well.

4.4 Conclusions and implications for management

The findings of this study revealed similarities in the composition of orders, butterflies and water insects of pristine, drained and newly rewetted bogs in South-Eastern Norway. Nevertheless, drainage altered the abundance of three individual orders, and the differences persisted for two orders despite rewetting efforts. Rewetting therefore appear unable to counteract most drainage inflicted changes in abundances within the first five years.

It is important to bear in mind that this order-based study only provides an overall understanding of general changes within the insect community following bog rewetting. The species diversity within each order makes it difficult to properly evaluate the effects of rewetting on communities without any further information on lower taxa. The inclusion of species would make it possible to evaluate more subtle differences among treatments. Therefore, before deciding on the achievements of Norwegian bog rewetting, additional assessments with indicator species of multiple orders should be carried out.

The use of indicator species, like the four specialist butterflies were initially meant to represent in this study, can provide further information about the ecological conditions of rewetted bogs and which other species might be present. However, even if the physical conditions have been successfully restored in a bog, it is not given that all species manage to reestablish. If desired species are missing following the reestablishment of conditions and habitats, the management meets the dilemma of whether to actively reintroduce the missing species or let nature take its course. Active reintroduction of flora is a common element in restoration practices of fens and bogs in several countries, but it is currently less widespread for fauna (e.g. Taillefer & Wheeler, 2012). Since the distance between pristine and rewetted bogs can impact the reestablishment of species, a prioritization of less isolated bogs might increase the positive effects on species diversity and reduce the need for further human interventions. Nonetheless, some changes in species composition will most likely persist between pristine and rewetted bogs, and it may be beneficial to properly define the expectations associated with satisfactory restoration of pristine-like insect communities.

Finally, this short-term study is only capable of assessing short-term effects on insects following rewetting. Bog restoration is often considered to be a slow and long process, and expectations of significant improvements within the first decade after rewetting might not be reasonable (Mitsch & Wilson, 1996). Longer-term studies over decades with repeated monitoring of rewetted bogs are therefore necessary before the effects, and possibly the success, of Norwegian

rewetting on the insect community can be determined. However, early and repeated monitoring of rewetted bogs can provide valuable information about the development, as well as detect lack of progression early in the process. This can call for adjustments of measures and save management both time and money (Mazerolle et al., 2006).

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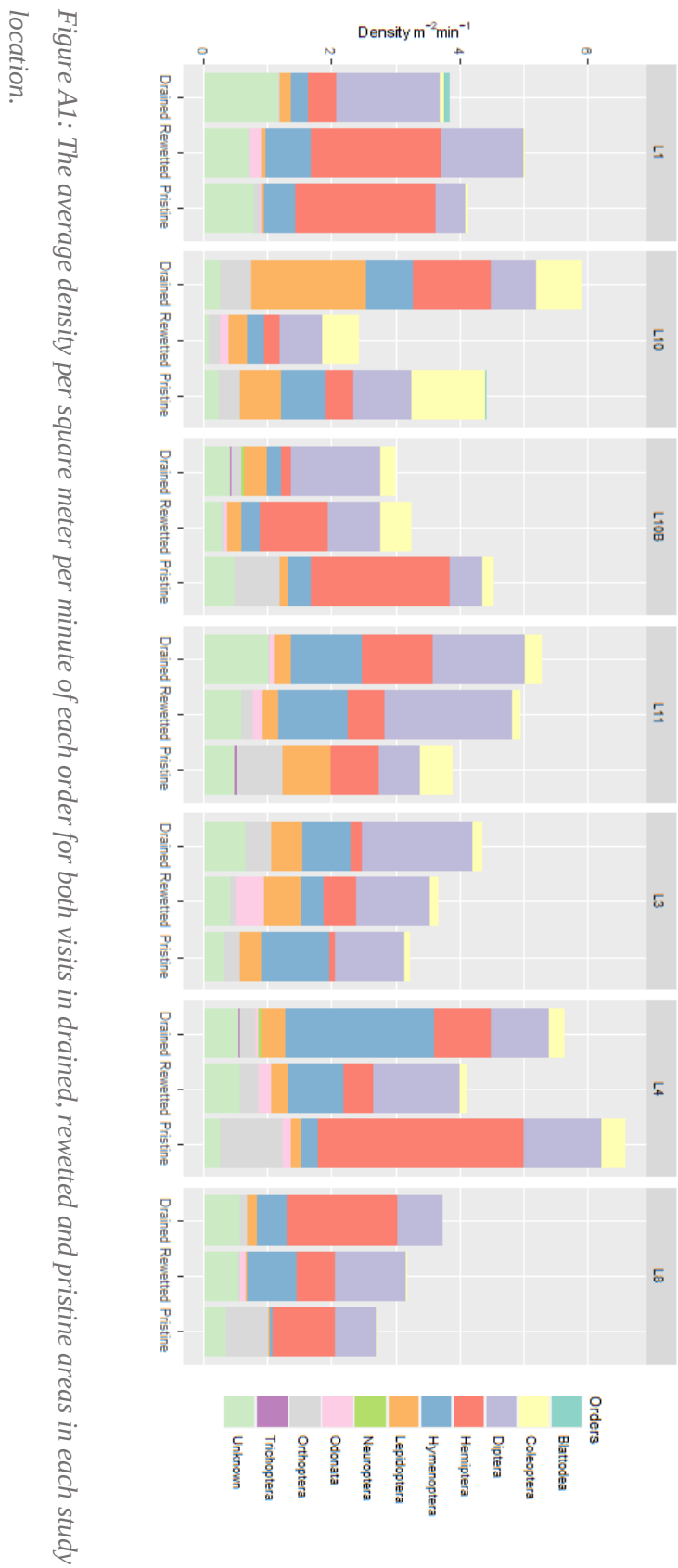
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Appendix A. Supplementary figures



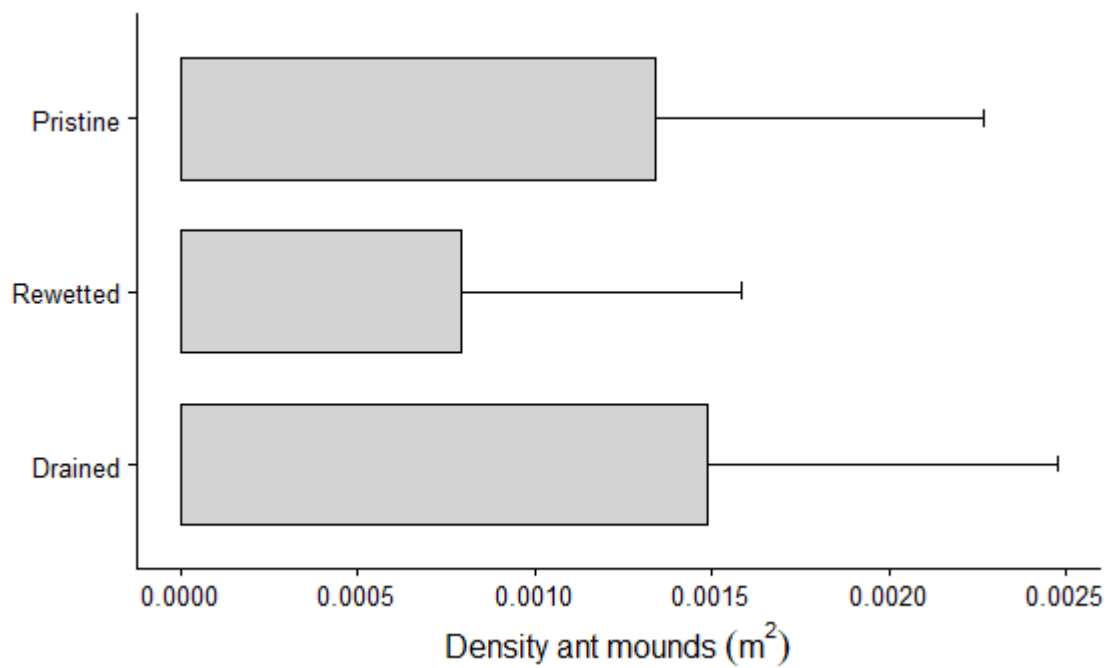


Figure A2: The average number of ant mounds per square meter in drained, rewetted and pristine bogs. The error bar represents the upper mean Standard Error (SE). Note that only eight ant mounds were registered and make up the figure.

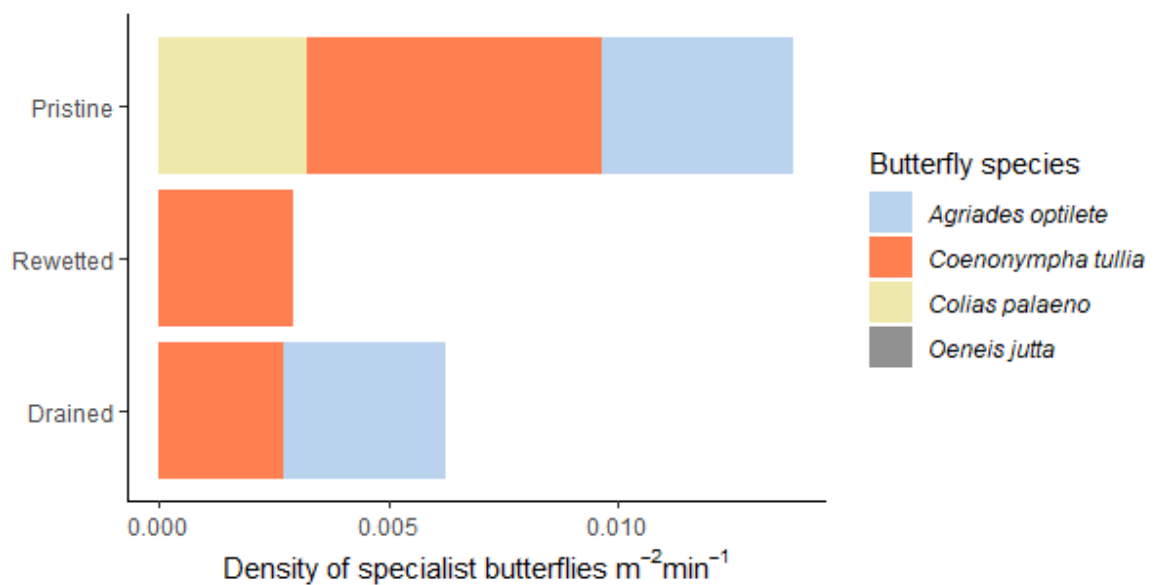


Figure A3: The average number of the target specialist butterflies per m² per minute in drained, rewetted and pristine bogs. Note that only seven target butterflies were registered during transect counts.



Figure A4: Mire specialist *Metrioptera brachyptera* found in the pristine area of L8 (Veggermyra N).

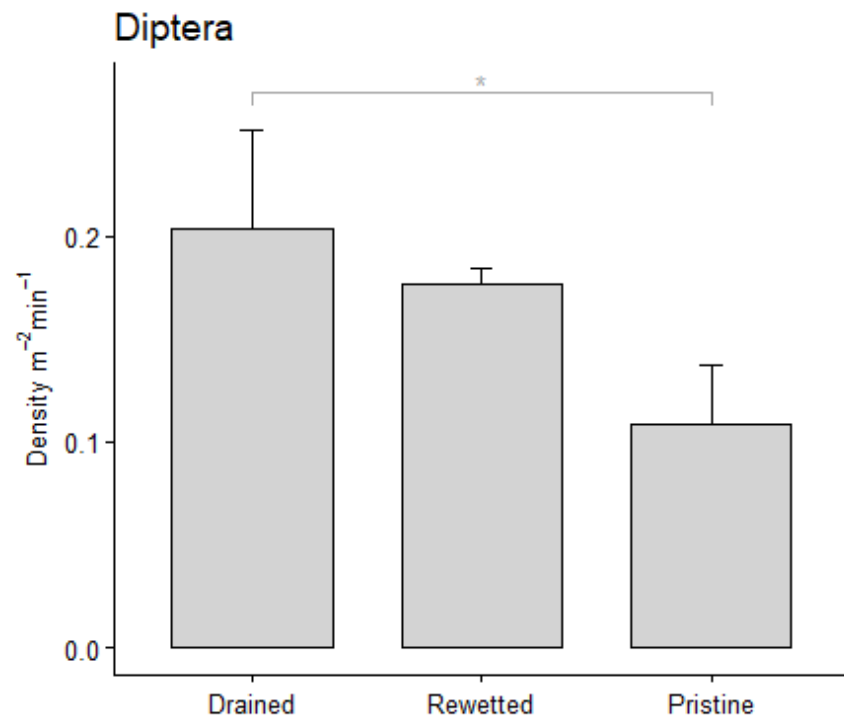


Figure A5: The average density of dipterans per square meter per minute for locations with pristine and rewetted areas within the same bog (L1, L3, L8). GLMM results showed a significant difference between drained and pristine bogs ($p = 0.02$), and the significance level is marked with stars in the plot (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$).

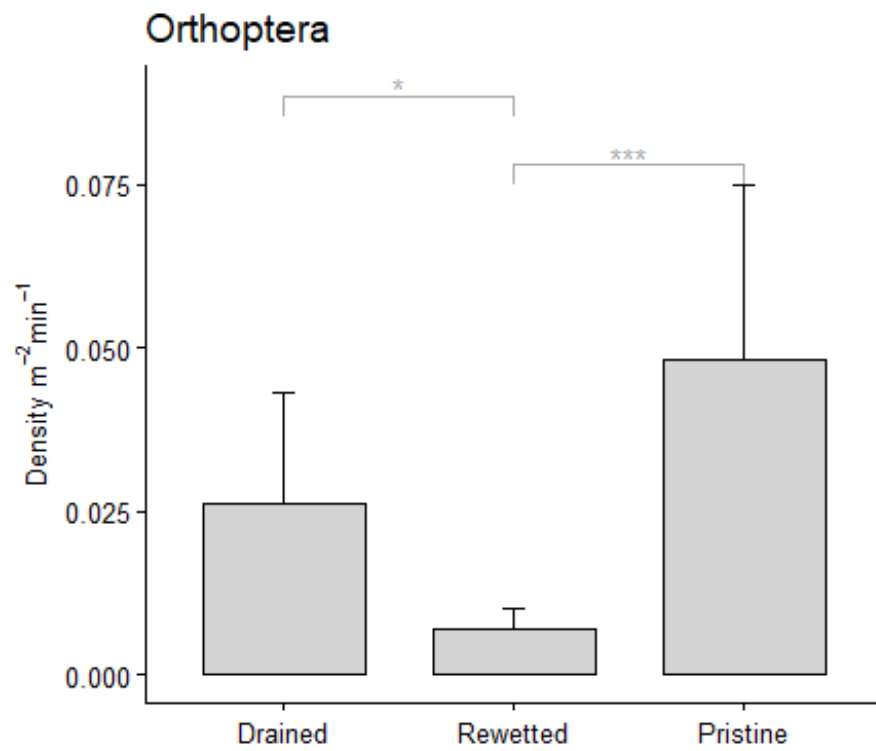


Figure A6: The average density of orthopterans per square meter per minute for locations with pristine and rewetted areas within the same bog (L1, L3, L8). GLMM results showed a significant difference between drained and rewetted bogs ($p = 0.04$) and pristine and rewetted ($p < 0.001$). The significance level is marked with stars in the plot (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$).



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