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Master's thesis in Natural Resources Management Supervisor: Martijn L. Vandegehuchte Co-supervisor: Sidonie I. E. Loiez May 2024

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SAMMENDRAG

Den alpine tundraen er spesielt sårbar ovenfor effekten av global oppvarming sammenlignet med andre økosystemer. Noen av disse effektene, som migrering av planter oppover fjellet, har allerede blitt studert i flere år, men andre, som effekten varme har på hele insektsamfunn er mindre studert. Hvis man også tenker på tilleggseffekten av bladsopp, som også påvirkes av oppvarming og som både positivt og negativt interagerer med insekt, er det gjort enda mindre forskning. Vi testet hvordan oppvarming kan interagere med endringer i bladsopp med å endre insektsamfunn i alpine tundrasystem. Vi samlet insekt med gule, blå og hvite fat-feller (pan-traps) i plotter utsatt for oppvarming og bladsoppreduksjonsbehandling i en full-faktorial utforming på tre forskjellige høyder i Dovre fjellområdet i Trøndelag, Norge. Oppvarming ble funnet å ha en negativ effekt på forekomsten av insekt på den laveste og midterste høyden, mens bladsoppreduksjon ble ikke funnet å ha noe effekt på mengden insekt. For sammensetningen av insektfamilier hadde både oppvarming og bladsopp en effekt, men de interagerte ikke. Midlertidig ble oppvarming og bladsoppreduksjon funnet å interagere for noen familier, som den samlede gruppen med Muscidae og Anthomyiidae, og for Phoridae, der det hadde en positiv effekt. Familiene som ble undersøkt reagerte ulikt på effekten av varme, bladsoppreduksjon og deres interaksjon. Endringen i insektfamilie- og artsmengde og sammensetning som et resultat av et varmere klima, som igjen kan føre til økning i bladsoppskader, kan føre til endringer i planter og andre dyrs tilstedeværelse og kan endre hele det alpine tundraøkosystemet. Dette i kombinasjon med de allerede kjente effektene av at planter og større dyr migrerer oppover i fjellet kan på sikt bety store endringer i den totale sammensetningen av arter, og derfor også endre deres interaksjoner.

ABSTRACT

The alpine tundra is especially vulnerable to the effects of global warming compared to other ecosystems. Some of these effects, like the migration of plants upslope, have already been studied for many years, but others, like the effects warming has on entire insect communities are less studied. In addition, foliar fungi can both directly and indirectly interact with insects, and they have been shown to be affected by climate warming. However, little research has been done on the impacts of climate change on the interactions between fungi and insects. We tested how warming might interact with changes in foliar fungi in altering insect communities in the alpine tundra systems. We collected insects using yellow, blue and white pan-traps in plots exposed to warming and foliar fungi reduction treatment in a full factorial design at three different elevations in the Dovre mountain area in Trøndelag, Norway. Warming was found to have a negative effect on the abundance of insects at the lowest and middle elevation, but foliar fungi reduction was not found to have a significant effect on insect abundance. For the composition of insect families, both warming and foliar fungi had an effect, but they did not interact with each other. However, warming and foliar fungi reduction was found to interact for some families, like the combined family of Muscidae and Anthomyiidae (MuscAntho) and Phoridae, where the positive effect of warming was stronger in the fungi reduction treatment. The insect families investigated differed in the effects of warming, foliar fungi reduction and their interaction. The change in insect family abundance and composition as a result of warmer climate, which may lead to increased foliar fungal damage, could cause changes in plant and other animals' presence and abundance, changing the entire ecosystem of the alpine tundra. This, in combination with the effects already known of plants and larger animals migrating up the mountains, could eventually mean large changes in overall species composition and abundance, and therefore ecological interactions.

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Table of contents

Figures

Tables

Abbreviations

1 INTRODUCTION

By releasing greenhouse gases into the atmosphere, humans have caused ongoing climate changes. (Houghton, 2005). The effects that global warming can cause are many, as a warmer climate could affect a great many species and ecosystems, that in return could impact humans, who depend on ecosystem services provided by biodiversity. The alpine regions, as well as the arctic tundra, boreal forests, rainforests, are some of the environments that are greatly affected by global warming (Seddon et al., 2016). Temperatures at higher elevations and latitudes increase in some cases more than at lower elevations and latitudes (Wang et al., 2014). Alpine species are already living on the border of tolerable habitats and physiology (Dahlhoff et al., 2019), so small changes in the ecosystem, like temperature and nutrient availability, can have large effects. A warmer climate can also lead to habitat loss, change and fragmentation (Koot et al., 2022) This has also been shown in alpine systems, where warming and abandoned grazing has led to upward migration of shrubs, causing loss of lichen cover (Vanneste et al., 2017). The alpine tundra usually refers to a landscape above the tree line and can be found either in high elevations or at high latitudes. The living conditions there are harsh, with high winds and low temperatures leading to low rates of decomposition and a short growing season. The low decomposition makes the soil more nutrient-deficient. These factors lead to lower diversity of species, but the species present that tend to be highly adapted to the habitat (Bliss, 1962). This makes it harder for other species to invade the tundra. Globally, arctic and alpine ecosystems are becoming increasingly dominated by shrubs and are losing lichen cover, which could cause ripple effects across the ecosystem, like reindeers reliance on lichen as a food source (Vanneste et al., 2017). Not only can global warming have an effect on specific species, but it can also threaten entire ecological communities as species are moving to higher altitudes and latitudes, joining local alpine and arctic species, for which it is difficult to migrate to cooler places (Gottfried et al., 1999; Rasmann et al., 2014).

As the climate warms, plants and other organisms such as animals and fungi might migrate upward in the alpine ecosystems to follow their thermal optimum. Alternatively, they might follow the plant species they depend upon as the plants migrate. Therefore, this upward migration of plants of various shapes and colors could cause the migration of other life forms, such as insects and fungi. Different insect species interact with different plant species and this has even caused insect species to respond differently to different colors and light, depending on the color their preferred host plants' leaves or flowers (Weiss, 1946).

Like plants, insects are also migrating to higher elevations, as has been found for beetles (Dahlhoff et al., 2019). The general trend for herbivores is higher abundance, and in some cases diversity, at intermediate elevations, and less at higher and lower elevations in the mountain, as abiotic factors limit the high mountain, and herbivory and predation limit the lower mountain (Moreira et al., 2018). Interactions are often stronger at lower elevations (Moreira et al., 2018), as the climate is less harsh and more competition is possible. A change in species composition has been found for a butterfly family in the Alps where there was a shift with elevation in which species in a family was present (Bonelli et al., 2021). Earlier reports of different families connected by Menéndez (2007), show a latitudinal and elevation migration, up and down in both elevation and latitude for *Lepidoptera*, while *Anisoptera*, *Neuroptera*, *Heteroptera* and *Orthoptera* only had an upward migration in elevation and latitude. Moths feeding on Larch move up in elevation, not as a response to warming overall, but due to warmer winters (Johnson et al., 2010). Bumblebee abundance has been found to be decreasing in lower latitudes as they migrate further north (Kerr et al., 2015), with larger bumblebees doing better in colder temperatures (Kenna et al., 2021). Alpine aquatic insects are modeled to be negatively affected by warming, more so in lower alpine elevations than higher elevations (Timoner et al., 2021), although aquatic insects are thought to have a postponed effect of warming as the water provides a buffer (Shah et al., 2020). Previous studies have found insect herbivory to decrease with elevations, linking it to plants being tougher as to handle the harsher climate (Rasmann et al., 2014). Plant defenses have been found to decrease with increased elevation, but also increase (Moreira et al., 2018), so it is not always a set respond to elevation. Another study along an elevation gradient from 1950 to 2440 m asl done over 30 years (1990 to 2020) found that some grasshopper species decreased in abundance, some increased and some stayed the same. A part of this variation was attributed to a significant temperature increase during the summer, also increasing development speed of nymphs (Illich & Zuna-Kratky, 2022). Furthermore, as the plant community composition changes, shifts in insect community composition could follow.

A change in plant community composition and climate could also affect rates of foliar fungi, which can greatly affect plants, while plants can also affect fungi (Rodriguez et al., 2009). Like insects, foliar fungi are affected by plant species composition (Borer et al., 2015; Liu et al., 2022; Whitaker et al., 2022). Therefore, both climate change and plants' upward migration, could affect foliar fungi. Total abundance of some foliar fungi would be expected to increase with increasing warmth and humidity (Talley et al., 2002), as foliar fungi have been found to increase in some plant species with increased warming and precipitation (Gaytán et al., 2022;

Liu et al., 2019; Talley et al., 2002). However, the evenness, richness and diversity of foliar fungi have been found to decrease with warming (Faticov et al., 2021). As the diversity of foliar fungi is higher at higher elevations (Liu et al., 2019; Ni et al., 2018), warming could therefore decrease the diversity of foliar fungi while increasing the abundance of foliar fungi. However, negative effects of warming on foliar fungi abundance have also been found (Randriamanana et al., 2015), as well as no effect of warming on foliar fungi (Kivlin & Rudgers, 2019).

Foliar fungi, like herbivory, can decrease photosynthesis, by covering the leaf, and steal nutrition from the plant (Fang et al., 2021; Udayanga et al., 2020), making it less healthy, which could make the plant less attractive to pollinators (Mauck et al., 2010). Reversely, plant damage in general could increase the plants growth and tolerance (Moisan et al., 2020; Röder et al., 2011), and make the plant create volatiles that deflect herbivores, decreasing herbivore damage (Clement et al., 2011; Röder et al., 2011). In other instances, foliar fungi create volatiles that attract insects (Boucias et al., 2012), thought to be a way to increase transmission, as foliar fungi are often transmitted by insects (Franco et al., 2021) and other animals, wind and water (Arnold & Herre, 2003). Foliar fungi may also benefit from herbivory because it gives them an opportunity to enter plant tissues through damage in leaves created by herbivores (Flessa et al., 2022), although they can also enter through the stomata (Currie et al., 2014). The alpine tundra is characterized by strong shifts in both biotic and abiotic conditions with small increases in elevation, and is one of the biomes most strongly affected by global warming. It is therefore an ideal ecosystem type to study how insect communities at different elevations respond to warming and changes in foliar fungi.

Norway, having several alpine areas as well as arctic tundra in the north (Seddon et al., 2016), might therefore be greatly affected by global warming. In Norway the average temperature has increased by $\sim 1.1^{\circ}\text{C}$ from 1900 – 2016, and precipitation has also increased by 20 % (met.no, 2024), with an estimated added increase of 4.5°C and 18 % precipitation by 2100 if business as usual continues (Hanssen-Bauer et al., 2015). The species that inhabit these alpine areas are adapted to the harsh climate, and a move toward warmer climate could shift the species composition. Small woody shrubs dominate the system, with species like *Betula nana*, several *Salix* sp., and ericaceous plants such as *Vaccinium* sp., in addition to grasses and sedges. The species might reproduce by vegetative reproduction or seeds, and pollination by wind. Pollination by larger animals, like birds and mammals or insects, is present for some plants to secure sexual reproduction (Rose, 2024). As the areas get warmer the limitations for other species could decline, meaning more competition for the native, specialist species (Michelsen et al., 2011). This could be problematic for the species adapted to the cold, as they might not have any direction to move to escape the climate that is too warm. Plants, insects and foliar fungi are all affected by a warmer climate. Warming could decrease the diversity of fungi. The species composition of insects could change, both as a result of warming but also as a result of a change in foliar fungi. These organisms could move up at different speeds, leading to mismatches between different species. The speed of migration for other organisms might therefore increase as the habitat becomes more suitable, as fungi migrating up the mountain could provide some fungivore insects with a food source, or migrating insect herbivores could provide local foliar fungi with easier access to leaves.

Climate warming, and changes in foliar fungi abundance potentially, and in some cases do, affect alpine insect communities. The prevalence of foliar fungi in alpine areas might also be influenced by warming. How warming in alpine areas affects insect communities and how warming might interact with foliar fungi abundance to alter insect communities, however, has not before been investigated. With this research we therefore addressed the following research questions:

- 1. How does warming affect alpine tundra insect communities?
- 2. How does the presence of foliar fungi affect alpine tundra insect communities?
- 3. Do warming and foliar fungi interact in their effects on insect communities?
- 4. Are some insect families affected differently from others?

The questions were answered by counting and grouping the insects into families, and assessing the amount of fungal damage on plants leaves.

As the climate becomes warmer, it is thought that the community composition of insects will change, probably showing an increase in the abundance of insects for some families and a decrease for others. Some insect families do better with fungi than other families as some eat foliar fungi, while other insect families prefer plants with less fungi. Other insects are not affected by foliar fungi. It can therefore be hypothesized that areas with more foliar fungi will change insect community composition. As climate warming affects fungi by increasing infection, and fungi affect insects, the effect fungi have on some insects will be stronger under warming. The effect of warming, foliar fungi and their interaction will not be the same for all insect families as herbivore and fungivore insects could increase with warming and foliar fungi, large insects could decrease with warming and some insects, like parasitical or nectar eaters, might not be affected by either.

2 MATERIALS AND METHODS

The project was conducted along a western mountain slope in the municipality of Oppdal, county Trøndelag, in Norway. The experiments were conducted at three different sites with three elevations: 1151m (N 62.29746, E 9.62976), 1352m (N 62.30553, E 9.65095) and 1540m (N 62.30759, E 9.67548) asl. At the lower, site the vegetation is mainly composed of shrub specieslike *Betula nana*, *Empetrum nigrum* and *Vaccinium vitis-idea* and abundant lichen cover. At the middle site a mixed vegetation of shrubs like *B. nana*, and herbs, sedges and grasses like *Carex bigelowii*, *Anthoxanthum nipponicum* and *Potentilla crantzii*. The higher site consisted of shorter plants like *Harrimanella hypnoides*, *Salix herbacea* and *Poa alpina*.

Treatments and setup of plots and sub plots follow the protocol provided from BugNet. BugNet is *"a global collaborative research network that aims to better understand the impact of invertebrate herbivores and pathogenic fungi on plant communities and ecosystems"* (bugnet.org).

2.1 Setup

For each elevation there are 6 plots, with 3 control plots, only treated with water, and 3 fungi reduction plots, treated with fungicide. In total 18 plots. Each plot is a square with side lengths of 5 m, composed of 4 square subplots with side lengths of 2.5 m. The treatments were applied to the plots 3 times during the summer on dry days: $29th$ of June for highest site and $1st$ of July for the middle and lower site, $22nd$ of July and $17th$ of August. Within each of the plots, an Open-Top Chamber (OTC) was placed in one of the subplots. It actively warms the soil and vegetation by an average of: 1°C for the highest elevation; 1.1°C for the middle elevation and; 0.2° C for the lowest elevation (See appendix 2 for visuals on temperature). The warming chambers are hexagonal shaped, with angled sides (60°) and indentations along the lower edges of each side panel to allow crawling animals to access the inside of the chamber. The OTCs were made by following the ITEX manual (Center & Copenhagen, 1996) and using the same size ratio. The base lengths of the side panels are 86.6 cm (see appendix 1.1). The OTCs were placed in a random subplot, in random corners of the subplot as the chambers did not cover the entire subplot. A total of 36 subplots were sampled: 12 per elevation.

2.2 Leaf sampling

Plants were sampled at the end of the growing season, September $12th$ – September $14th$. The leaves were used to assess the fungal damage in the plots to investigate how foliar fungi reacted to warming at the different elevations, as well as to see whether the fungi reduction treatment worked. The plants were sampled in all the subplots mentioned above.

For each subplot, a maximum of five plant species was sampled, starting with the plant species that had the largest coverage, until the sum of the coverage of the species sampled reached 80%. If the species with the highest coverage value covers 90% of the subplot, only that species was sampled. As the subplots did not contain the same plants, the 5 most dominant plant species in the separate subplots were sampled, regardless of plant species identity. For the individual samples, all individuals of the species were sampled if there were less than 10 species. If there were more than 10, 10 random individuals were chosen. Problematically, some plants, like shrubs, grow vegetatively, and the base of the stem might be located outside of the plot, but the plant might cover almost the entire plot. We then defined an individual as one branch. We collected the entire individual/branch, and then took 5 random leaves in the lab. 10 branches or individuals per plant species were collected. For each of the 10 individuals, 5 leaves were used to visually estimate the percentage of damage.

2.2.1 Damage estimation

In the lab, five grown leaves were investigated to estimate the percentage of fungi coverage and herbivory damage. Sometimes fewer leaves and individuals were screened as some plants had already started senescing. The estimation was done using a stereomicroscope to be able to see the fungal and herbivory damage, as the leaves were often small, and the amount of damage present was also small. For plants with less than five leaves, all leaves were looked at. For shrubs, at least 25 leaves per species were assessed for damage, dead leaves were not taken into account. The pathogenic fungi were observed as red/yellow dots (rust), pale green/yellow to brown areas (downy mildew), small dots that can be brushed away (powdery mildew), discolored plant tissue (leaf spots), and as "other". "Other" are types of damage we could not specify. The stated fungi were the most common and therefore directly estimated to a fungal group. The herbivory damage was seen as holes, lines or dots on the leaves. The visual scan, or estimation, was done by estimating the percent cover by looking at both sides of the leaf blades.

2.3 Insect sampling and identification

Insects were sampled, counted and identified to family level.

Insects were sampled at three different times during the summer: $8th - 10th$ of July, $27th$ $-29th$ of July and $21st - 23rd$ of August. That way both the insects that are earlier and later in the season could be sampled. During the experiment, the insects were collected using pan traps placed in two subplots in each of the plots. One was placed inside the warming chamber, and one outside, about 3.5 m away from the other, in the diagonally opposite subplot. The pans had three different colors as to attract different types of insects: white, yellow, and blue (Vrdoljak & Samways, 2012). The pans were round plastic bowls with an approximate size of 15 cm diameter and 5 cm deep. As well as the different colors, the pans were painted with UVfluorescent paint as to attract insects (Vrdoljak & Samways, 2012). The pan traps were placed, with one of each color, on a stand created with a wooden pole and metal wire lowered into the ground. The height of the stand was hard to control as the ground was rocky, and the poles were of a specific height, leaving the pans ranging from as close to the ground as possible to approximately 15 cm above the ground.

In the pan traps we added soapy water, until the pans were about 2/3 full, and left them for approximately 48 hours. The soap in the water breaks the surface tension, making the insects fall into the water and drown instead of standing on it (Russo et al., 2011). The soap water was then poured out through a fine sieve, to capture the insects, and the insects were funneled into a tube with ethanol (70%). The soapy water was made using Neutral soap, with a small drop into each pan. The tubes were marked with elevation, plot, subplot, color, and date. In total 324 tubes were used. See appendix 1.1 for pan-trap setup.

After sampling the insects were studied in a laboratory using a stereomicroscope, with the insects put in water in a petri dish. They were sorted into family, or if this was not possible to order, and counted. The data was then added into a spreadsheet document (Appendix 1.2). For the insects that were difficult to identify, the order and a number was assigned as to separate them.

2.4 Data analysis

After all the data was collected and added into spreadsheet documents, it was analyzed using R version 4.2.1.

2.4.1 Fungal damage

The amount of herbivory damage was not enough to be meaningfully analyzed and was therefore removed from the dataset. Some damage amount of all the fungal groups was observed.

Total fungal damage was calculated by adding together the different damage percentages of the different fungal groups and was used in the analysis. Then the average damage percentage was calculated per plant individual or branch, before calculating the average per species. Then this damage averages per species were further averaged per plot. These percentage data were then analyzed using a binomial model, provided by the "lme4" package. The total damage was added as a cbind() into the model. To allow for percentages with one digit after the decimal point (i.e. tenths of percents) it was multiplied by 10, after which it was rounded to the nearest whole number, leaving it to look like this: cbind(rounded, thousand), where "thousand" is a column only containing the value 1000. Warming, fungi reduction, elevation and all their interactions were added as fixed effects, and plotted as a random effect:

• Damage model \lt - glmer(cbind(number multiplied with 10 and rounded, thousand) ~ Warming * Fungi reduction * Elevation + (1|Plot), family = binomial(link $=$ "logit")

Type II Wald chi-square test, with a "Kenward-Roger" method for denominator degrees of freedom were used to test the significance of fixed effects, using the Anova() function from the package "car".

2.4.2 Insect data

Before doing any analysis, the insect numbers were summed across the three sampling times for each subplot, after which any families that occurred in fewer than 9 plots observations were removed (i.e. the number of replicate subplots per treatment combination after summarizing the 3 times insects were sampled). The 3 times were summarized instead of averaged to get the total number of insects and families per treatment through the season. Further cleaning was needed to remove the pans that had fallen over from the data, and the ones that were marked wrong. Incorrect marking happened in one of the subplots at one of the sampling times, so the two subplots for that plot were removed. Pans falling over happened 5 times in total, so these were removed. See appendix for table.

The model chosen for the data was a negative binomial, as it, like a Poisson, is good for count data, but better for data that is over-dispersed. Insect abundance was added as the response variable and warming, fungi reduction, elevation and pan-color were added as fixed effects, as well as all their interactions. Plot was added as a random effect. The model then looked like this:

• Insect_model < - glmer.nb(Number ~ Warming * Fungi reduction * Elevation * Pan.color + $(1|Plot)$

The above model was also used to analyze the abundance of a few dominant insect families, to see if families differ from each other in the response to warming and fungi reduction and the interactions. Fixed effects in the models of total and per-family insect abundance were tested as for the model of fungal damage.

To look at the effect of the treatments on the composition of insect families, a Nonmetric Multidimentional Scaling (NMDS) ordination was done using metaMDS() from the "vegan" R package. To do this, the data had to first be transformed into a matrix, having the families as separate columns. This was visualized using geom point in ggplot from the "ggplot2" package. This matrix was also used in a permanova using the adonis2() function with a strata argument for the plots to get the significance of the differences in insect composition for the different treatments and their interactions. Pairwise post-hoc tests were conducted using the emmeans() function with a FDR argument, to see the significance of the treatments for the different treatment interactions.

3 RESULTS

A total of 2455 leaves were investigated, and 16905 insects identified.

The p-values not found in the Anova tables in the main text can be found in the emmeans() in the appendix (2.1 for fungi data, and 2.2 for insect data).

3.1 Fungal Damage

The overall amount of fungal damage on the leaves was low, as can be seen in figure 3.1.1, ranging from under 1 % to under 10 %. The damage is significantly higher in the lower plot (L, $p = 0.004$, appendix 2.1.2), with non-significant difference ($p = 0.9$, appendix 2.1.2) between the highest (H) and middle site (M). The fungi reduction treatment did not have a significant main effect on damage, but it did interact significantly with elevation. This results from a clear reduction in fungal damage in the fungi reduction treatment as compared with the control treatment for the lower site ($p = 0.15$, appendix 2.1.3), and an increase for the higher site ($p = 0.16$, appendix 2.1.3). Warming, fungi reduction and elevation also showed a significant three-way interaction in the effect on fungal damage, where the higher site has a lower damage percentage in warming chamber in the control treatment compared to the fungicide treatment where the damage is higher inside the warming chamber ($p = 0.06$, appendix 2.1.4).

Figure 3.1.1 Average percentage fungal damage in each treatment combination along three elevations: low (L), medium (M) and high (H). The letters on the bars for standard error indicate significant differences according to post-hoc pairwise comparison after FDR correction.

Table 3.1.1 Anova result from the three-way binomial model of the effects of warming, fungi reduction, elevation and their interactions on fungal damage percentage averaged per plot (3 per elevation).

3.2 Insect number and composition

3.2.1 Total insect abundance

For the effect on the number of insects, there is a difference between the different elevations, with lower overall numbers at the lowest elevation, which is visible in Figure 3.2.1.1. There is also a difference between the different pan trap colors, with the color interacting with the elevations, as the white pan trap had more insects in the higher site, and the blue in the lower site. The main effect of warming had a significant effect on insect number, with there being fewer insects in warming chambers for the lowest elevation ($p = 0.0001$ for the lowest elevation, appendix 2.2). The effect of warming in the middle elevation is not significant within the treatments ($p = 0.1$, appendix 2.2) for warming within control nor for the fungi reduction plot ($p = 0.1$, appendix 2.2), but when looking at the main effect of warming it is significant ($p = 0.01$, appendix 2.2). When comparing non-fungicide + non-warming with fungicide + warming, it is also significant ($p = 0.003$, appendix 2.2). Warming interacted with elevation, where the effect of warming is not significant for the high elevation. The fungi reduction treatment was not found to have an effect on the total number of insects. However, the p-value ($p = 0.072$) is still low for the interaction between fungi reduction and elevation, which can be seen in the bar-plot for the middle site where the control plot has a higher number of insects compared to the fungi reduction plot if we total warming and non-warming, the p value there being 0.015. Warming and fungi reduction treatment did not interact in the effect on insect number.

Table 3.2.1.1 Anova of a four-way negative binomial model of the four fixed effects (Warming, Fungicide, Elevation and Pan.color) and their interactions, from insect abundance. Values are rounded.

Figure 3.2.1.1 The Number of insects precent in each treatment, C (control), F (fungi reduction) with or without warming (1,0) for three pan colors in three elevations, low (L), intermediate (M) and high (H). The number being of three sampling times (early, mid and late summer) added together. Different letters above the standard error bars, indicate significant difference at $p = 0.05$ level after FDR correction.

When looking at the most abundant insect "family" from the samples, MuscAntho (the grouped Muscidae and Anthomyiidae), seen in figure 3.2.1.2, warming and elevation interact, as the effect of warming is stronger at the lower elevation. Fungi reduction and elevation also interact with the effect of fungi reduction being positive at the lower elevation and negative at the middle elevation. Warming and fungi reduction also interact significantly ($p = 0.07$, appendix 2.3.1), as there are overall more insects in the warming chamber compared to outside the chamber in the fungi reduction plot compared to in the control plot. There is a very strong interaction between elevation and pan color as there is a shift from higher abundance in the blue traps at the lower site to higher abundance in white traps at the higher site. Comparing the barplot (figure 3.2.1.2 of MuscAntho) to the one of total insect abundance (figure 3.2.1.1), we can see that over half of the insects are MuscAntho.

For Chironomidae, both warming and fungi reduction affect the number of individuals negatively, both interacting with elevation where the effect of warming was higher at the higher sites, and the effect of fungi reduction was higher at the middle site. For Phoride, see Appendix 2.3.2, we observed a very strong interaction between warming and elevation, as the negative effect of warming is much stronger in the lower and middle site compared to the higher site. Warming and fungi reduction also interacted, with the effect of warming being smaller in the fungi reduction plots, however, neither a main effect of fungi reduction, nor fungi reduction interacting with elevation, had a significant effect. For Sciaridae (Appendix 2.3.5) neither warming nor fungi reduction interact with elevation, and they do not interact with each other. Interestingly warming, fungi reduction and elevation interact for Sciaridae, as we can see an opposite effect on the higher site compared to the lower site: In the higher site warming has a negative effect in the control plot but a positive effect in the fungi reduction plot, but in the lower site warming has a positive effect in the control plot but a negative effect in the fungi reduction plot. The trend of pan color effects shifting with elevation is the same for Cecidomyiidae (Appendix 2.3.3) as for MuscAntho. Chalcidoidea and Ichneumonidae (Appendix 2.3.5 and 2.3.6), both being wasps, prefer the yellow pan traps as did Chironomidae, but only Ichneumonidae had an effect of warming, with warming being negative, although less negative at the highest site.

Figure 3.2.1.2 The Number of insects of three dominant families precent in each treatment, C (control), F (fungi reduction treatment) with or without warming $(1, 0)$ for three pan colors in three elevations, low (L) , intermediate (M) and high (H). The number being of three sampling times (early, mid and late summer) added together. Letters are added to above the standard error bars, showing which treatments are similar or not across all elevations.

3.2.2 Insect composition

Fungi reduction and warming had a significant effect on the composition of insect families. Warming and fungi reduction did not interact, but both warming and fungi reduction did interact with elevation, meaning different insect families respond differently to the effects at different elevations. Pan color also affected insect family composition. This can be seen in the ordination of pan-trap color per elevation, where the white in the lowest elevation is different from blue in the lowest elevation. Blue for the highest elevation overlap a lot with white at the lowest elevation, where blue and yellow for the highest elevation also overlap, with white at the highest elevation being more dissimilar. Yellow at the middle elevation has the biggest ellipse, and overlap, to some degree, with all the other ellipses, while still being different from them. Pan color also interacted with warming. The difference in composition can be seen in the ordination plots (Figure 3.2.2.1) where the points with and without warming are not placed at the same place, creating a circle that moves in a different direction from the nonwarming circle. It also differs for the different elevations, where warming at the lower elevation is further to the top left. The same is true for the control vs fungi reduction, where the direction of the circles are different for the three elevations, with the lowest elevation being more dissimilar from the other elevations. Many of the families are close to the center, indicating limited variation in the abundance of these families, with some families moving further away,

such as the Psylloidea and Cicadellidae to the top left, the same direction as the warming chamber and the lowest elevation, and Scathophagidae and Chironomidae to the bottom right prefer the yellow pan trap in the non-warming plot in the middle elevation. All of them are moving away from the fungi reduction treatment. MuscAntho is not located far from the middle but slightly to the top-right, the same direction as fungi reduction, without warming. It looks to be no preferences for the fungi reduction treatment.

Warming and fungi reduction did not interact in the effect on insect composition. The warming subplots for the middle elevation are similar to the lowest elevation without warming, indicating a similar insect family composition. There are stronger community dissimilarities at the lowest and middle elevation regarding warming, and not as much for the highest elevation. Warming at the highest elevation fall within warming at the middle elevation, meaning the composition is similar, but less variable for the highest elevation as the circle is smaller. The yellow pan-traps at the lower and middle elevation have large ellipses, meaning many families, with high abundance, were collected in them. The blue ellipses are smaller. The lowest elevation has the largest ellipses for the fungi reduction plot, located further to the left, similar to the two other plots. Control and fungi reduction mostly overlap, but for the middle elevation control and fungi reduction does not overlap as much, indicating a shift insect families.

Table 3.2.2.1 The Adonis results from an adonis2 model showing the change in composition of insect families with different treatments and their interactions, up to a four-way interaction.

yellow (Y) , white (W) and blue (B), per elevation. 3) fungicide treatment per elevation; control (C) **Figure 3.2.2.1** Ordinations based on insect families from a metaMDS. 1) values from the three elevations and the warming treatment, warming (1) , non-warming (0) . 2) the three pan-trap colors: yellow (Y) , white (W) and blue (B) , per elevation. 3) fungicide treatment per elevation; control (C) and fungicide (F) . elevations and the warming treatment, warming (1), non-warming (0). 2) the three pan-trap colors: **Figure 3.2.2.1** Ordinations based on insect families from a metaMDS. 1) values from the three and fungicide (F).

4 DISCUSSION

4.1 Effect of warming on insect abundance and composition

Warming, interacting with elevation, was found to both influence insect abundance and composition, which was expected, with the effect being stronger on composition compared to abundance. The group MuscAntho was by far the most abundant group of insects and could be driving the effects on total abundance of insects. As the ordinations show, the ellipses (visualization of the similarities of datapoints) for the middle and high elevation (warming and non-warming) overlaps a lot with the non-warming ellipse at the lower elevations, indicating that the warming plots and the lower elevation could be more similar. This would also make sense with the average temperature inside the warming chamber for the middle elevation is the same as the average temperature for the low elevation without warming at 11°C. There is still a visual difference between warming and non-warming within all three elevations, with the smallest difference being at the highest elevation. The ellipse for non-warming treatment at the lowest elevation overlaps more with the warming at the middle compared to warming and nonwarming at the middle elevation overlapping. This could be an indicator that a warming chamber is a good representation for how a shift in insect composition might shift with warming as they migrate up in elevation and that warming will make higher elevations more similar to the lower site.

The effect of the warming treatment was not present in the highest elevation, but was for the middle and lowest elevation when it comes to insect abundance (appendix 2.2). The warming treatment worked better at the middle and high elevation, so the low response of insects at the highest elevation could be because insects that prefer warmer environments simply are not present at that elevation. However, some families, like Chironomidae, have a lower number of individuals in the warming chamber in the highest elevation, meaning some families are affected but not all. Perhaps it is because competition is an important interaction that affect many species, but might not be as present at the highest elevation. Warming itself at the lower elevations might not be the main driver, but instead how warming indirectly causes effects on insects, from changing plant composition and making the habitat more suitable for some insect species whom other insects interact with. This could also be affecting the soil, which could affect insects (Murdoch et al., 1972; Robinson et al., 2018). Therefore, it would be possible to think that the effect the warming treatment had on the lowest elevation could be the effect it will have further up if the climate warms further. Possibly was the effect warming now has at the middle elevation previously present as the lowest elevation, and the composition of insects have already shifted. Two herbivore insect groups, Cicadellidae and Psylloidea, prefer the warmed plots at in the lower elevation, as is also found by previous studies, where herbivory increases with warming (Illich & Zuna-Kratky, 2022; Moreira et al., 2018; Rasmann et al., 2014).

4.2 Effect of fungi reduction on insect abundance and composition

The fungi reduction treatment did not have an effect on total insect abundance, but there was almost a significant ($p = 0.07$, Table 3.2.1.1) interaction between the effect of fungi reduction and elevation. This would be expected as the fungi reduction treatment seemingly only had a noticeable, yet non-significant effect on foliar fungi on the lower elevation ($p =$ 0.15), possibly because of the overall low amount of fungal damage. It must be mentioned that the fungicide itself could have an effect on insects directly, although the fungicide used here have a low toxicity. Though taking this into consideration, the direct effects of fungicide would be present for all elevations, and that there would not be a difference between the elevations. The effect also differed among the families, further implying that the fungicide was not the cause. It was expected that foliar fungi would affect the composition of insect families, which was found, but only in interaction with elevation. We also found that different insect families are differently affected by foliar fungi reduction treatment. As the abundance of fungi was generally low, and given that the fungicide is probably never able to completely remove all foliar fungi from a system, it is not entirely unexpected that the lowered abundance of foliar fungi and/or inspection of a larger number of leaves per plot, this difference would have been significant. It must also be mentioned that we did not sample the same plant species at the three elevations, therefore there could be an effect of plant species that we did not take into account. Some plant species might be infected by fungi at different times of the season, and some plant species more than others (Faticov et al., 2021). The plants found at the middle site were the plants that had gone the most into senescence, as there were fewer evergreen plant species compared to the lower and higher elevation. The plants sampled, even though they were the most dominant, might not be the ones that are the most important in insect interactions, and might therefore not represent the interactions the best. An example of this could be *Betula nana*, as it is not insect-pollinated (De Groot et al., 1997), although insect herbivores still feed on it, at low intensity (Barrio et al., 2017).

4.3 The interaction of warming and fungi on insect abundance and composition

It was expected that warming and fungi reduction would interact in the effect on insect abundance and composition, as warming was thought to make the effect of foliar fungi stronger, which was not found. This could be explained by the low amount of fungal damage observed on plants. It could also be that warming did not affect foliar fungi that much, as has been found previously (Faticov et al., 2021; Kivlin & Rudgers, 2019). The exact effect of the warming chamber, except for it increasing the temperature, is unknown. We don't know if it also made it dryer inside the chamber, which could be negative for foliar fungi, as fungi like moist and warm environments (Talley et al., 2002). However, not all foliar fungi need a warm and moist environment (Liu et al., 2019; Penuelas et al., 2012), and as we did not find a negative effect of the warming treatment on the foliar fungi, it suggest that warming did not impact the living conditions of the fungi. The chamber did not influence the plant species present for this first season of implementation.

As there is a difference in dominant plant species among the three elevations, it is possible that the presence of different plant species affected the fungi and insect community composition. The general temperature difference among the three elevations could also explain the differences in composition, especially as the insect abundance and composition differed among the three elevations. However, as we did not have replicate sites at each of the elevations, I cannot make any statement on the overall effect of elevation, only that for these elevations at these locations there was a difference. For some families the interaction of warming and foliar fungi reduction was present, although it was only present for the middle elevation, but we did not find an effect of the fungi reduction treatment at the middle elevation. It is difficult to know why it was only present there, and I cannot think of a good explanation for it. It might because the middle elevation had the highest amount of dead/senescent leaves, or that the most dominant plant species are not the ones that have the most foliar fungi, so the insects could have still reacted to the reduction of foliar fungi. The highest elevation seemingly has fewer interactions overall, of both warming and fungi reduction, which relates to research finding that interactions are stronger at lower elevations (Moreira et al., 2018).

4.4 Is there a difference between different families?

Muscidae and Anthomyiidae, are very abundant flies with a broad niche, where some are detritivores, fungivores, dung eaters, and some eat nectar, while larvae often feed on decomposing matter, fungi, plants or are predatory (Gomes et al., 2021; Grzywacz et al., 2017). Phoridae are also abundant flies, some being dung eaters, other fungivores, herbivores, detritivores or predators (Disney, 2012). Chironomidae are mosquitoes, where some adults either do not feed or feed on feces, nectar or honeydew. They do not feed on blood, and do not live long in adult form (Armitage et al., 2012). Cecidomyiidae are galling midges, meaning they lay their eggs on leaves as galls, where the larvae feed on the pant tissue or are predators, and adults feed on honeydew and nectar (Gagné & Jaschhof, 2004). Sciaridae are gnats, where the larvae feed on many things such as plants, decaying matter and fungi, and adults feed on nectar (Carvalho-Fernandes, 2016). Chalcidoidea is a group of very diverse wasps where some are parasitic and the larvae develop in other insects' larvae, egg or pupae, some feed on plant matter, while some make galls (Munro et al., 2011). Ichneumonidae is another very diverse family of parasitic wasps, laying their eggs in other insects' larvae, with adults feeding on plant sap and nectar, or in some cases the fluids of hosts (Klopfstein et al., 2019). These parasitic wasps are also thought of as pollinators, which the flies feeding on nectar can also be.

Insects were identified to family or higher level. The particular species composition of families or higher-level groups could have varied substantially among our plots and treatments. This is perhaps what we can see in the change in preference in color. Higher abundance of insects in the white pan-traps at the highest site were found for four families: MuscAntho, Phoridae, Cecidomyiidae and Sciaridae. One explanation could be that the vegetation is different, and the flower color changes with elevation, with more white flowers higher up and more purple and blue flowers further down. The species higher up would therefore be adapted to prefer the color white, and the ones lower down would prefer bluer colors. When looking at the dominant plant species, listed in the appendix 2.1, we see that none of the species dominant lower down are present at the highest elevation. Of the shrubs found lower down, many have purple flowers. The plants at the higher site were plants of all three colors: white, yellow and purple. If warming then continues, and changes the flora, this would indirectly affect the insects as the species adapted to the whiter flowers would have to migrate with the plants until they reach the summit where they cannot move upward any further, or no longer maintain their interactions (Vanneste et al., 2017). These species could then be lost due to warming. Another addition is that in some cases species are attracted to specific plants or color because of sexual

selection, where they have adapted to mate on some flowers for niche separation (Noriyuki, 2015), which can also explain the shift in preferred flower color.

It was mentioned that no interaction between warming and fungi reduction was found for insect number or composition, but it was found for MuscAntho, which tells us that MuscAntho alone did not drive the result for the total insect abundance. Why they interact in this case is difficult to know, as no effect of warming on fungal damage was found, but perhaps there was an effect on fungi that we could not see on the leaves. Alternatively there could have been an interactive effect of warming and fungi on the plants that MuscAntho reacted to, for exemple by affecting flower size, nectar production or volatile production. The same interaction was also found for Phoridae, and both MuscAntho and Phoridae are flies that eat dead organic matter. It is possible that the fungi reduction treatment also decreased the abundance of nonfoliar fungi. For example, if there are fewer fungi that decompose organic matter there will be less food for these flies. This hypothesis, however, remains to be tested. In the other families no interaction between warming and fungi reduction was found. Indeed, most of the insects from the other families are not necessarily decomposers or herbivores, although it is surprising that fungi reduction did not have an effect on Sciaridae, as these are typical feeders of fungi. It could be that the overall abundance of fungi is so low in our study system that the insects do not rely on it as a food source, instead eating other things. For most of the tested families warming has either a negative effect, as was also observed for the total abundance of insects, or has no effect. Cecidomyiidae is the only family for which warming had a positive effect, maybe because warming increases reproductive success, as more of the larvae survive with warming, increasing the abundance of insects (Illich & Zuna-Kratky, 2022).

It would have been interesting to test the effect of warming and fungi on the abundance of more insect families, but the numbers of insects were not that high, considering that for even some of the most dominant families we only found an average of 2 insects per trap. Investigating how warming and fungi reduction would affect pure nectar-feeders and herbivorous insects would be interesting, especially with research finding an increase in herbivorous insects, and general insect abundance, with warming (Dahlhoff et al., 2019; Illich & Zuna-Kratky, 2022; Moreira et al., 2018). It would be expected that herbivorous insects are more affected by fungi compared to mosquitoes, as mosquitoes do not eat fungi like some herbivores do (Eberl et al., 2020). How fungi would interact with warming in its effect on herbivorous insects would be advantageous to know for future research, also regarding agriculture, as herbivory and pathogens affect food crop production negatively. The amount of nectar-feeding and herbivorous insects sampled was unfortunately too low to use for an analysis, however, it is interesting to note that most of them were found at the lowest elevation. The low abundance of herbivore insects corresponds to low amount of herbivory damage found in the leaves.

4.5 The effect of the fungicide and the OTC

When sampling plants, for all the elevations, some of the plants had gone into senescence. Therefore, many of the samples were not used, leading to a smaller sample size than initially intended. There was no overall effect of the fungi reduction on fungi damage on leaves, which can be explained as the overall percentage of fungal damage on the investigated leaves was very low, although higher at the lower site. The low damage on the higher elevations, and more damage at the lowest elevation supports previous studies about how warming positively affect fungi, as it range from warmer lower down to colder further up (Liu et al., 2019; Talley et al., 2002). This suggests that warming could lead to the migration of foliar fungi. An alternative explanation to the lower fungal damage amount at the highest elevation could be that plants at higher elevations are better adapted to handle stresses like foliar fungi and herbivory (Moreira et al., 2018; Rasmann et al., 2014).

Another aspect that needs to be mentioned is that the OTC warming chamber could have an effect on both the fungi and the insects. Either by being a physical barrier for fungal spores and insects, or by being shiny. Some insects, like bumblebees, fly close to the ground at times (Combes et al., 2023; Spaethe et al., 2001), and might therefore avoid flying into the chamber and rather fly around it. The fungal spores could be stuck inside the chamber, increasing abundance within the chamber, as well as hindering spores from entering into the chamber. The effect of the chamber itself was not tested, and therefore cannot be completely excluded. The chamber could also cause a different microclimate that insects might select for or against, and therefore not give an actual representation of the effects of climate warming.

5 CONCLUSION

As the preference for color changes in elevation, and if this effect is representative of the Dovre area, warming climate could lead to the loss of the species that prefer the whiter colors as, these colors could be lost, unless they adapt to these colors. Warming will change both the composition and number of insects present, depending on the elevation. The abundance of fungi is likely to increase at higher elevations as fungi migrates up the mountain with warmer temperatures. This was however not found with the warming chamber, but as the fungi damage was higher at the lowest elevation it is still a likely possibility. An increase in fungi abundance could potentially also cause changes in the composition of insect families, as well as changes in the abundance of some families like Muscidae, Anthomyiidae and Phoridae. A change in the composition and abundance of these very dominant families could alter the presence of other plants and animals that are dependent on these insects for pollination, or as a food source. If the change in insect families happens faster than for plants, the plants at higher elevations could lose interactions they depend on. An increase in fungi could be an increase in food sources present in the alpine system for some insect species, like fungivores, and herbivores that also feed on fungi (Eberl et al., 2020), which could negatively impact the attractiveness of plants to pollinators, or it could make the plants grow bigger and better as to compensate for the damage and threat posed upon it. With an increase in herbivory and pathogens pests increase, which are thought to migrate to higher elevations and latitudes (Wang et al., 2021). This could lead to earlier than predicted loss of species. Hence, management of these ecosystems should be considered if we don't want to lose them. As stated by Shah et al. (2020): "Thus far, research on high-elevation insects has been limited, due in part to the difficulty of accessing alpine areas, with little known of their endemic communities and how they are being altered.", also stating that further research is needed. This project is part of the research looking into this topic.

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Appendix

1 Methods

1.1 Setup

The three blocks represent each elevation, meaning there were three blocks per elevation. The figure showing one plot illustrate how they looked, with one of the subplots having the OTC in it. The warming chamber is also illustrated, as well as photo of one pan-trap-trio inside a chamber taken in the field.

1.2 Dataset

Table 1.2.1 was used for the binomial model of foliar fungal damage per treatment and elevation. As we can see, each plot has warming and no warming, and each elevation have 3 fungi reduction plots and 3 control plots.

Table 1.2.1 Rounded amount of foliar fungal damage in percent multiplies with 10 per plot and elevation for the different treatments (Fungi reduction and warming). C being without fungi reduction treatment and F with fungi reduction treatment, 1 being with warming and 0 without warming

Figure 1.2.1 show the number of insects in a family for each plot and treatment for the three elevations after the three sampling times had been summarized. This table was used in the 4-way negative binomial model for the effect of the treatments for the number of insects

Figure 1.2.1 A screenshot of the dataset for insects after cleaning it and taking the sum of three sampling times.

Figure 1.2.2 was used for the adonis2 test to see the effect of the different treatments on the composition of insects. A similar dataset, with only number of individuals per family, was used for the NMDS and then ordination plot.

Figure 1.2.2 A screenshot of a matrix dataset with different insect families being columns.

2 Results

Figure 2.1 Visualization of the temperature in Celsius outside and inside the OTC for the three elevations throughout the season when temperature loggers were in the field. This only represent the day (from sunrise to sunset).

2.1 Fungal damage

Table 2.1.1 was used to see the dominant species for the different elevations. The Damagecolumn shows the average amount of foliar fungi coverage for the different plant species.

Table 1.1.1 Percentage damage cover of foliar fungi for each plant species per elevation with the calculated standard error, and the color of the plants flower

Elevation	Species	Damage	Error	Color
H	Fjellfrostjerne, Thalictrum alpinum	0.00000000	NA	Purple/Yellow
H	Fjellkattefot, Antennaria alpina	1.17000000	1.19324915	White
H	Fjellrapp, Poa alpina	1.30000000	1.84691936	Purple/Green
H	Fjellsmelle, Silene acaulis	0.90350877	0.85988405	Purple/Pink
H	Flekkmure, Potentilla crantzii	2.97540984	2.70976948	Yellow
H	Geitsvingel, Festuca vivipara	0.42447917	1.01614794	Purple/Green
H	Moselyng, Harrimanella hypnoides	1.53000000	1.22808684	White
$\rm H$	Museore, Salix herbacea	9.97500000	5.81021107	Red
H	Oyentrost, Euphrasia officinalis	0.00000000	NA	White
H	Stivstarr, Carex bigelowii	0.86206897	1.43711170	Black
H	Trefingerurt, Sibbaldia procumbens	5.52884615	3.25667412	Yellow
L	Blokkebær, Vaccinium uliginosum	16.56000000	6.56818933	White/Purple
L	Dvergbjork, Betula nana	10.90625000	6.85015043	Yellow
L	Greplyng, Kalmia procumbens	2.88000000	3.52582039	Purple/Pink
L	Krekling, Empetrum nigrum	1.11818182	1.67434088	Purple
L	Sauesvingel, Festuca ovina	0.53947368	0.81071047	Purple/Green
L	Stivstarr, Carex bigelowii	0.75000000	0.55277080	Black
L	Tyttebaer, Vaccinium vitis-idaea	6.70652174	3.60311611	White/Pink
M	Blaalyng, Phyllodoce caerulea	3.27428571	3.18215639	Purple
M	Blankstarr, Carex saxatilis	0.04545455	0.08703883	Black
M	Blokkebaer, Vaccinium uliginosum	0.00000000	NA	White/Purple
M	Dvergbjork, Betula nana	12.37500000	5.21960901	Yellow
M	Fjellsmelle, Silene acaulis	2.11904762	2.04801066	Purple/Pink
M	Fjelltistel, Saussurea alpina	0.00000000	NA	Purple
M	Flekkmure, Potentilla crantzii	0.50000000	0.48304589	Yellow
M	Krekling, Empetrum nigrum	1.27200000	1.90835176	Purple
M	Moselyng, Harrimanella hypnoides	0.82000000	0.96422104	White
M	Rabbesiv, Juncus trifidus	0.00000000	0.00000000	Brown
M	Saetermjelt, Astragalus alpinus	6.83333333	3.36030753	White/Purple
M	Sauesvingel, Festuca ovina	0.41752577	0.57536283	Purple/Green
M	Slirestarr, Carex vaginata	1.57692308	1.15807003	Green/Brown
M	Tyttebaer, Vaccinium vitis-idaea	3.57142857	3.55090039	White/Pink

Emmeans of damage model, important interactions are highlighted.

2.1.2 Emmeans of the differences in damage between elevations

contrast estimate SE df z.ratio p.value H - L -0.7258 0.231 Inf -3.137 0.0040 H - M -0.0337 0.235 Inf -0.143 0.8860 $L - M = 0.6920 0.231$ Inf 3.001 0.0040 Results are averaged over the levels of: Warming, Fungicide Results are given on the log odds ratio (not the response) scale. P value adjustment: fdr method for 3 tests

2.1.3 Emmeans for effect of fungi reduction treatment per elevation on percentage damage.

2.1.4 Emmeans for interactions with warming, fungi reduction and elevation on percentage damage.

2.2 Insect number emmeans

The emmeans() is done with the 4-way interaction model, adding the different fixed effects I wanted to look at. The most useful numbers are highlighted. Significant values $(p<0.05)$ highlighted in yellow. **1)** insects per elevation **2)** insects per elevation and fungi reduction treatment **3)** insects per elevation and warming **4)** insects per elevation with fungi reduction and warming.

1 $\mathcal{D}_{\mathcal{A}}$ contrast estimate SE df z.ratio p.value H - L 0.4347 0.0819 Inf 5.307 <.0001 H - L 0.4347 0.0819 Inf 5.307 <.0001
H - M -0.0706 0.0799 Inf -0.884 0.3766
<mark>L - M -0.5053 0.0794 Inf -6.361 <.0001</mark> -0.5053 0.0794 Inf -6.361 <.0001 Results are averaged over the levels of: Warming, Fungicide, Pan.color Results are given on the log (not the response) scale. P value adjustment: fdr method for 3 tests contrast estimate SE df z.ratio p.value H C - L C 0.45915 0.117 Inf 3.938 0.0004 H C - L C 0.45915 0.117 Inf 3.938 0.0004
H C - M C -0.21381 0.111 Inf -1.926 0.0812
H C - H F -0.00163 0.116 Inf -0.014 0.9888 H C - H F -0.00163 0.116 Inf -0.014 0.9888
H C - L F 0.40863 0.113 Inf 3.608 0.0009 $H C - L F$ 0.40863 0.113 Inf H C - M F 0.07092 0.113 Inf 0.627 0.6120 L C - M C -0.67296 0.113 Inf -5.952 <.0001 L C - M C -0.67296 0.113 Inf -5.952 <.0001
L C - H F -0.46078 0.118 Inf -3.892 0.0004 L C - L F -0.05052 0.115 Inf -0.438 0.7083 L C - M F -0.38824 0.115 Inf -3.375 0.0016 M C - H F 0.21218 0.113 Inf 1.879 0.0822 M C - L F 0.62244 0.110 Inf 5.679 <.0001
M C - M F 0.28473 0.109 Inf 2.603 0.0154 0.28473 0.109 Inf 2.603 0.0154
0.41026 0.115 Inf 3.564 0.0009 H F - L F 0.41026 0.115 Inf 3.564 0.0009 H F - M F 0.07255 0.115 Inf 0.631 0.6120 L F - M F -0.33771 0.112 Inf -3.025 0.0047 Results are averaged over the levels of: Warming, Pan.color Results are given on the log (not the response) scale. P value adjustment: fdr method for 15 tests

2.3 Dominant families

For the seven dominant families, both the figures and an anova of the four-way model is based on insect abundance. The figure shows the number of insects, summarized for the three sampling times and averaged across plot (3 plots per treatment). This is for the three elevations high (H), middle (M) and low (L), with control (C) and fungicide (F), and warming (1) or not warming (0).

2.3.1 "MuscAntho"

2.3.2 Phoridae

2.3.3 Cecidomyiidae

2.3.5 Sciaridae

2.3.7 Ichneumonidae

