ACKNOWLEDGEMENTS

ABSTRACT

Alpine ecosystems are particularly expected to experience changes due to temperature rise, but little is known how insect herbivory may respond to that process.

I used two already established study sites at different elevations with control plots and Open Top Chambers (OTCs) in a Dryas octopetala *heath in the alpine ecosystem of Finse, southwestern Norway, to investigate whether experimental warming does affect insect herbivory. Leaf feeding damage was recorded in early and late summer and number of insect herbivores counted by searching the plots; pitfall traps were used to map other potential insect herbivores in the area. General Linear Models (GLMs) were used to examine the effects.*

Experimental warming increased the total amount of insect herbivory, mainly due to plant species Dryas octopetala *and* Bistorta vivipara. *Most insect herbivores were Lepidoptera and* Zygaena exulans *was the most abundant species. Larvae of* Z. exulans *were found in higher number inside as compared to outside the OTCs. The pitfall traps indicated other potential insect herbivores.*

This study suggests that some plant species such as Dryas octopetala *and* Bistorta vivipara, *are more susceptible than others to insect herbivores with temperature rise. Concluding that insect herbivory may have important impact on species composition and ecosystem functions.*

Table of contents

1 INTRODUCTION

Climate change influences most of earth's ecosystems (Parmesan & Yohe 2003; Parmesan 2006). Those at northern latitudes and high altitudes, corresponding to arctic and alpine environments, are particularly expected to experience changes due to temperature rise (IPPC 2007; Parmesan 2006). Global mean temperatures have increased and the warming is predicted to continue (IPPC 2007), indicating temperature as one of the main drivers of climate change (Bale et al. 2002).

Climate warming research has mainly been studied in plants (Arft et al. 1999; Elmendorf et al. 2012a; Elmendorf et al. 2012b; Walker et al. 2006; Wolkovich et al. 2012), predicting plant responses to be an important driver of alpine plant species' diversity due to warming climate (Sala et al. 2000), which may even cause a decline in biodiversity (Elmendorf et al. 2012a; Elmendorf et al. 2012b; Parmesan 2006; Walker et al. 2006).

Plants responses to warming may be (1) changed phenology such as advanced greening and flowering (Arft et al. 1999; Liu et al. 2011), (2) changed distribution (Parmesan 2006), (3) altered reproduction rate (Arft et al. 1999) and/or (4) changes in plant abundance (Elmendorf et al. 2012b; Liu et al. 2011), in combination with altered cover of plant species (Liu et al. 2011), which may affect species composition thus community diversity (Klanderud & Totland 2005; Walker et al. 2006). However plants responses in a plant community may vary between species (Klanderud 2008) and functional groups (Arft et al. 1999).

In general, temperature affects insect herbivores, directly due to impacts on physiology and behavior (such as development, population dynamics, range of

distribution and abundance) and indirectly due to changes in the host plant (Bale et al. 2002).

Some studies have been focusing on the above mentioned direct impacts of temperature on insect herbivores, conducting for instance experiments with artificial warming (e.g. Adler et al. 2007), studies along altitudinal/latitudinal gradients (Hodkinson & Bird 1998) and studies about the synchrony between plant and insect herbivores (e.g. Hill & Hodkinson 1995).

Effects of experimental warming which have been found on insect herbivores are (1) changes in phenology (Liu et al. 2011), (2) increase in insect development and reproduction potential (Ayres 1993; Ayres & Lombardero 2000; DeLucia et al. 2012; Harrington et al. 2001; Malmström & Raffa 2000) and/or (3) changes in abundance of insect herbivore species (Dollery et al. 2006; Liu et al. 2011). Most of insect herbivores may advance their larvae emergence (e.g. Visser & Both 2005) while other may delay (Liu et al. 2011). Some insects might also increase its geographical range as moving upwards in alpine areas (Dieker et al. 2011) or moving towards north (Bale et al. 2002). Insect species feeding on a wide range of different host plants (polyphagous insect species) are considered to be less affected by global warming than insect species feeding only on one or two plant species (mono- or oligophagous insect species) (Bale et al. 2002). The overall trend of most insect herbivores to warming is an increase in abundance (Bale et al. 2002; Harrington et al. 2001).

Only few studies have been focusing on the interaction between plant and insect herbivores (e.g. DeLucia et al. 2012; Richardson et al. 2002; Roy et al. 2004). Experimental warming may change trophic relationships between plants and insect herbivores (Liu et al. 2011). That change in trophic relationships may be due to changes in the phenology and/or abundance of both plant and insect herbivore species (Liu et al. 2011). In that case, possible consequences of increased insect herbivory may be (1) reduced reproductive capacity in some plant species like lower production of seeds (2) changed plant species composition and (3) may lead to the

loss of some plant species (Liu et al. 2011). Additionally, climate warming may cause a mismatch in synchrony between plants, as host- and food plant, and the insect herbivore (Both et al. 2009; Hegland et al. 2009). All together, they may change ecosystem properties in a long term perspective (Liu et al. 2011).

These possible consequences of insect herbivory at the species- and community level underline the importance of studying the interaction between plants and insect herbivores.

I specifically ask the following questions:

- Does experimental warming affect the amount of insect herbivory?

- Does insect herbivory vary between plant species, under experimental warming?

- Does experimental warming affect the number of insect herbivores?

2 MATERIALS AND METHODS

2.1 Study area

The study was conducted during the summer of 2012 (June to August) in the alpine ecosystem of Finse (60°36'N, 7°31'E), southwestern Norway, which belongs to the Hardangervidda mountain plateau. Climate is oceanic with cool summers and high precipitation (Moen 1998). Mean monthly temperatures and precipitations during the study period were 6.2°C and 86 mm (at 1224 m a.s.l.), and annual values were -2.1°C and 1030 mm, respectively (The Norwegian Meterological Institute 2013).

The study area was in the southwest slope of Mt. Sandalsnuten (ca. 1550 m a.s.l.), which is a *Dryas octopetala* heath dominated by wintergreen dwarf shrub (*Dryas octopetala*) and is also relatively rich in other plant species (Klanderud & Totland 2007), including forbs (*Bistorta vivipara* and *Sausurea alpina*) and dwarf shrubs (*Salix reticulata* and *S. herbacea)*. The macro-Lepidoptera (*Boloria napaea* and *Erebia pandrose*) (Lepidoptera.no 2013; Solhøy 1997) and the moth Mountain burnet (*Zygaena exulans*) (Hågvar 1976; Lepidoptera.no 2013; Solhøy 1997) are observed within the study area and might represent the most important herbivores. In addition, *Melasoma collaris* L. is a dominant leaf beetle (Hågvar 1975; Solhøy 1997) at Finse, additionally, a weevil (Curculionidae), a grasshopper (*Melanoplus frigidus*), some sawflies (e.g. Tenthredinidae) and several micro-Lepidoptera are also known herbivores from the area (Seglen 1967 cited in Hasle 2013; Solhøy 1997).

2.2 Study design

To examine to what extent temperature influences feeding damage caused by insect herbivores, two different elevations of different temperatures were used: a low-elevation site (leeside, ca. 1450 m a.s.l.) and a high-elevation site (ridge, ca. 1550 m a.s.l.). The high site is more exposed to wind, so the snow melts earlier and the growing season is around three weeks longer(Nybakken et al. 2011). The mean air temperature during summer 2011 (July and August) was 8.7°C (low site) and 7.5°C (high site); and mean soil temperatures (ca. 5 cm above ground) were 7.5°C and 7.2°C, respectively (Nybakken et al. 2011).

Both study sites were already established with control plots and OTCs. OTCs are a common method to study global warming in high-latitude and altitude ecosystems (Hollister & Webber 2000; Marion et al. 1997). The low site was set up in 2003 with 20 OTCs (Sandvik & Eide 2009) and the high site in 2000 with 40 control plots and 40 OTCs (Klanderud & Totland 2007). At both study sites, 10 control plots and 10 OTCs

with similar plant composition were randomly chosen and included in the present study. I gathered data from the high site, to compare with that of T. Hasle, another master student, who gathered data from the low site during the same summer (Hasle 2013).

OTCs in both sites were hexagonal with transparent polycarbonate walls (Klanderud & Totland 2007; Sandvik & Eide 2009; Fig. 1). Inner diameter at ground level was 0.92 m (low site) and 1 m (high site). Distance between OTCs and control plots was ≥ 1 m (low site) and ≥ 2 m (high site). OTCs increased mean air temperature 5 cm above ground level by ca. 1.5°C and soil temperature by ca. 1.0°C in both sites (Klanderud & Totland 2005; Sandvik & Eide 2009). This corresponds with an expected warming of 0.2-0.5°C per decade until 2050 for the Norwegian mainland (Hanssen-Bauer & Førland 2001).

OTCs are passive systems which means that the flow of energy is not technically controlled, thus the increase in temperature is mainly due to natural solar radiation (Hollister & Webber 2000; Marion et al. 1997) In addition, unwanted ecological effects are minimal regarding factors like light, moisture, gas exchange and wind (Arft et al. 1999; Marion et al. 1997) OTCs may prevent certain herbivores from entering, but they are not stuck into the ground (Hollister & Webber 2000) and thus not an impermeable barrier.
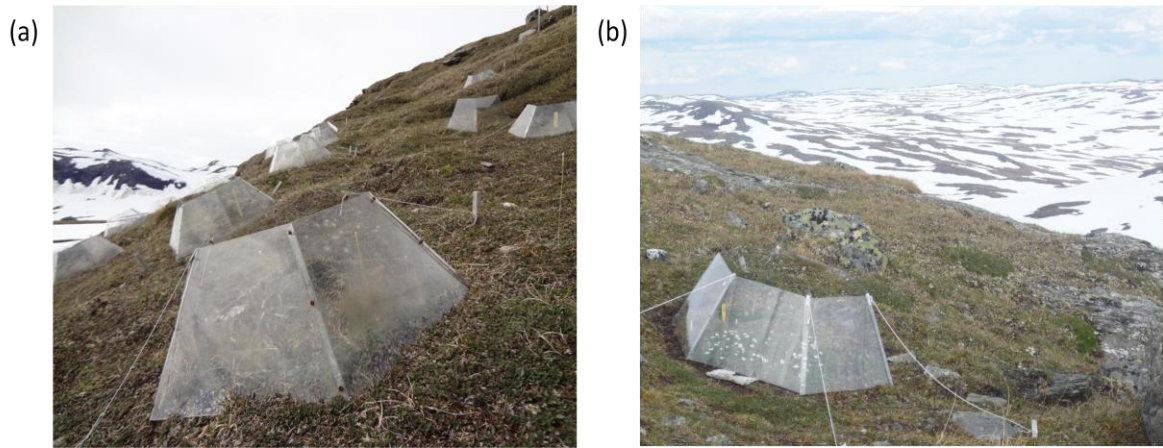
Fig. 1. OTCs (a) at the low site and (b) at the high site at Mt. Sandalsnuten, Finse, Norway summer 2012. Photo credit: (a) T. Hasle, (b) S. Bergmann.

The data was recorded during two different periods: early (both elevations: 19th-28th of June) and late season (low site: 1st-4th of August; high site: 28th of July to 1tst of August). The same control plots and OTCs were used during both seasons (a total of 80 plots).

To avoid edge effects and ensure replicability and consistency, I collected data from within a 50 x 50 cm frame placed in the middle of the control plot or OTC. This frame was divided into smaller subplots to facilitate data recollection. I searched for and identified herbivorous insects and noted their developmental stage (adult/larva). If a herbivore was not in the frame but in the OTC, I still recorded it, since they move fast. I did the same for insects next to the control plots. I removed no insects from any site to minimize impact and I took pictures of any unidentified species for later verification. Next, I recorded leaf feeding damage on the vascular plants caused by leaf-chewing insects and the following data: scientific name of plant and total amount of feeding damage. I focused mainly on *Dryas octopetala*, *Bistorta vivipara*, *Salix reticulata*, *S. herbacea* and *Sausurea alpina* as they were used within a feeding preference experiment in cooperation with T. Hasle (Hasle 2013). Those plant species were chosen, first, because they were observed to be the most common and even the

most fed on plant species within the study area. Secondly, previous observations indicated some of the above mentioned plant species as the preferred host plant of the insect herbivore *Zygaena* exulans (Hågvar 1976; Lepidoptera.no 2013), which was the most present Lepidoptera species in the study area, plus the study species within the feeding preference test.

Other species included: *Carex*, *Parnasia Palustris*, *Poa Alpina*, *Rannuculus Acris*, *Thalictrum Alpinum*, *Tofildia Pusilla* and *Vaccinium Uliginosum*. The whole process took at least one hour per OTC/control plot, while the time spent on searching for insects took approximately 15 minutes.

The 20th of June I set up five pitfalls in similar vegetation more than 10 m away from the OTCs and control plots at both sites to get a rough estimation of species and number of insect herbivores present. Each pitfall consisted of a small plastic cup with the bottom replaced by a fine mesh to act as a sieve, inserted into a larger one containing a mix of propylene glycol and soap. The traps were emptied every two weeks; 3rd of July, 28th of July and 11th of August. A plastic roof prevented rain from accumulating in the pitfall and diluting the liquid mix. The traps were emptied by replacing the small cup containing the insects and refilling the liquid mixture. Data from the five pitfall traps was pooled within each site to minimize work load, as the data should mainly be used to identify herbivore species at each site.

I brought all removed cups to the lab at the Finse Alpine Research Center, where I preserved the insects in 70 % alcohol and, separated them according to site and date. Later, I took them to the lab at the Norwegian University of Life Sciences (UMB), where an assistant identified genus/family as far as possible. The insects were grouped into: macro-Lepidoptera (adults), micro-Lepidoptera (adults), macro-Lepidoptera (larvae), Coleoptera (Chrysomelidae), with main focus on insect herbivores like *Zyganea exulans*, *Noctuoidea* and *Geometridae*, *Erebia pandrose*, *Tortricoidea* and *Chrysomelidae*.

2.3 Statistical analyses

The main herbivores observed were Lepidoptera larvae. In the statistical analysis, I used two variables; total number of *Zygaena exulans*, which was the most common larvae and the most frequently, found feeding, and total number of Lepidoptera. The total number of Lepidoptera included *Zygaena exulans*, *Noctuoidea* and *Geometridae.*

To test the effects of experimental warming on the total amount of feeding damage (response) a GLM was performed. Categorical explanatory variables were treatment (control, OTC), elevation (low, high) and season (early, late). In addition total number of *Zygaena exulans* and total number of Lepidoptera were used to explain the feeding damage.

To determine the effect of experimental warming on the total amount of feeding damage on *Dryas octopetala* or *Bistorta vivipara* I ran two GLMs with feeding damage of each plant species as a response variable. The model included treatment (control, OTC) as a categorical variable and plant species cover (%) as a continuous variable. Both models were only used for the high site (for the low site see Hasle 2013). In addition, both tests were only performed for the late season because the *Dryas octopetala* or *Bistorta vivipara* cover was only recorded then (data obtained from Siri Lie Olsen). I chose *Dryas octopetala* and *Bistorta vivipara* because they were observed to be the most fed on. However, *Salix reticulata* also showed leaf damage but the sample size was too low (only seven data points).

To test the effect of experimental warming on the relative amount of damage on *Dryas octopetala* or *Bistorta vivipara,* I performed two GLMs with data from the high site in the late season. The relative amount of feeding damage (response variable) was calculated as the total amount of feeding damage divided by the cover of each species (%). The models included treatment (control, OTC) as a categorical variable and the total number of *Zygaena exulans* and the total number Lepidoptera as continuous variables.

To determine how experimental warming affects the total number of *Zygaena exulans* or the total number of Lepidoptera (response) I performed a two GLMs with treatment (control, OTC), elevation (low, high) and season (early, late) as categorical explanatory variables.

Total amount of feeding damage, total amount of feeding damage on *Bistorta vivipara* and the relative amount of feeding damage of *Dryas octopetala* and *Bistorta vivipara* had to be log 10 transformed to reach normality. The total number of *Zygaena exulans* and the total number Lepidoptera were poisson-distributes. All other response variables fulfilled the criteria for normality. Every performed model included all possible interactions among the single factors but in terms of simplifying the model, insignificant factors were removed and limited two way interactions.
All analyses were performed using the fit model in JMP Pro 10 for Windows. A P-value of 0.05 or less is considered significant effect in the model.

3 RESULTS

Does experimental warming affect the amount of insect herbivory?

The GLM showed significant difference in the total amount of feeding damage between early and late season, with less damage in the early season (Table 1, Fig. 2a). Furthermore, there was a significant difference between OTCs and controls, with less damage in the controls (Table 1, Fig. 2b). Most feeding damage was recorded on *Dryas octopetala* (2517 cases) and *Bistorta vivipara* (1959 cases). *Salix reticulata* had 135 cases of feeding damage, with most of it recorded in the high site, whereas the 37 feeding damage on *Salix herbacea* was restricted to the low site. The 32 feeding damage on *Saussurea alpina* were recorded at both sites. Damage on the remaining plant species occurred at lower densities (Appendix 1).
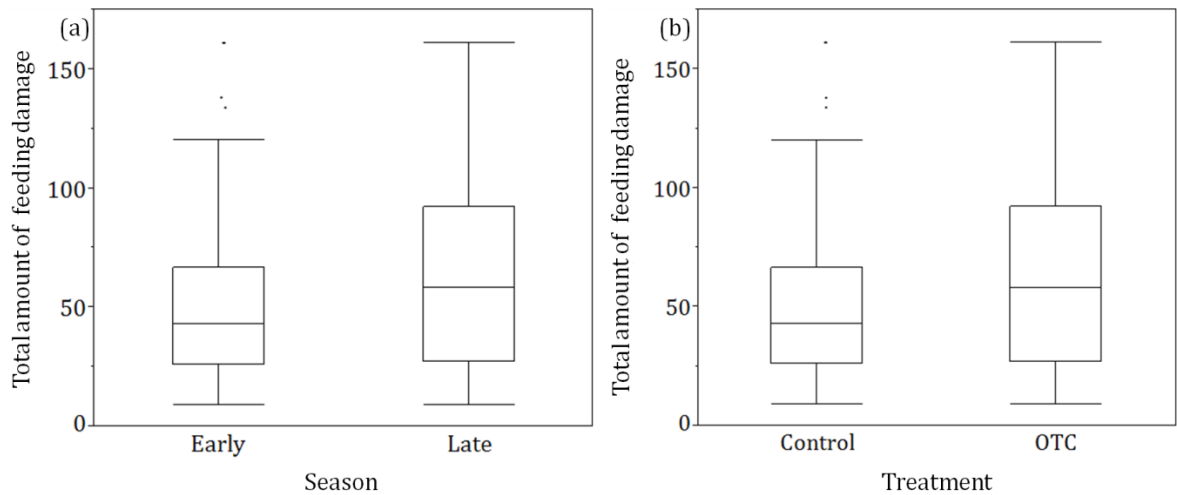
Fig. 2. Box-plots showing median of the total amount of feeding damage divided by (a) early and late season and (b) controls and OTCs for all data collected at the two sites at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 40 in each plot.

There was a close to significant interaction between season and *Zygaena exulans* with more larvae in the early season (Table 1, Appendix 2). Fig. 3 indicates an increase in feeding damage with number of larvae during early season, whereas no change in the late season.
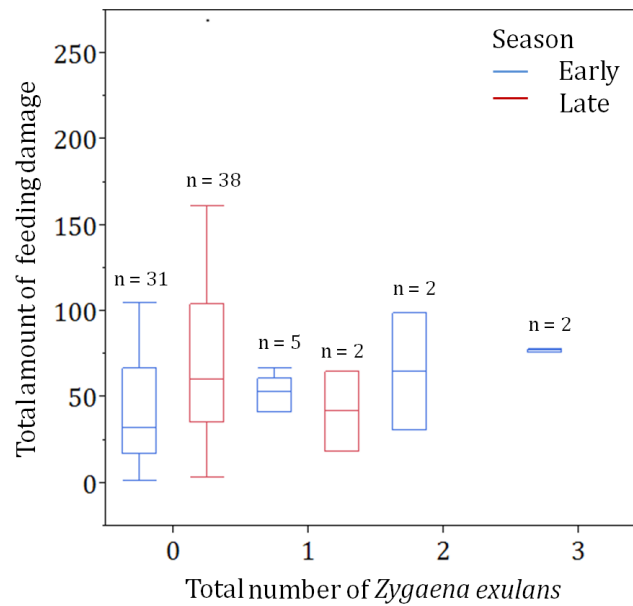

Fig. 3. Box-plots showing median of the total amount of feeding damage, interaction between seasons (early, late) and total number of *Zygaena exulans* at Mt. Sandalsnuten, Finse, Norway summer 2012.

There was no effect of site, total number of Lepidoptera or any of their interactions and the variables were removed from the final model (Table 1).

Table 1. GLM analyses of the total number of feeding damage for treatment (control, OTC), season (early, late), total number of *Zyganea exulans* and their interactions at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 80 in the analysis.

Parameters	Parameter estimate	F Ratio	P-value
Season	-0.10	4.43	0.039
Treatment	-0.13	9.79	0.002
Zygaena exulans	-0.04	0.08	0.771
Season*Treatment	0.03	0.42	0.520
Season**Zygaena exulans*	0.25	3.16	0.079
Treatment**Zygaena exulans*	0.12	2.04	0.157

Does insect herbivory vary between plant species, under experimental warming?

The GLM showed a close to significant effect of treatment on the total amount of feeding damage on *Dryas octopetala* (Table 2), with slightly more damage in OTCs than in controls (Fig. 4a, Appendix 1). On the other hand, treatment had a significant effect on the total feeding damage on *Bistorta vivipara* (Table 2), with higher damages in OTCs (535 cases) than in controls (179 cases) (Fig. 4b, Appendix 1).

Furthermore, there was a close to significant interaction between treatment and the *Dryas octopetala* cover (%) on the total feeding damage on *Dryas octopetala* (Table 2); Fig. 5 illustrates an increase in feeding damage with higher *Dryas octopetala* cover (%) in the OTCs, but not in the controls.

Fig. 4. Box-plots showing median of the total amount of feeding damage on (a) *Dryas octopetala* and (b) *Bistorta vivipara* in control and OTC for the late season at the high site at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 10 in each plot. Note the differences in scale at the y-axis.
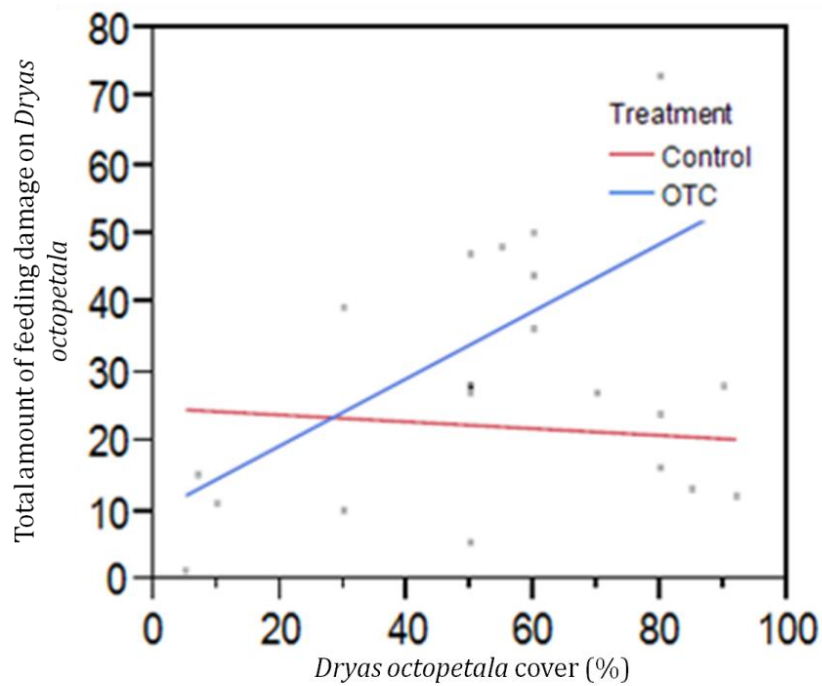
Fig. 5. Regression plot (r² = 0.40; p = 0.069) of the relationship of *Dryas octopetala* cover (%) and the total amount of feeding damage on *Dryas octopetala* in control and OTC for the late season at the high site at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 10 in each plot.

There was no significant effect of the *Bistorta vivipara* cover (%) (Table 2).

Table 2. GLM analyses for the total amount of feeding damage on *Dryas octopetala* and *Bistorta vivipara* with treatment (control, OTC) and cover (%) as explanatory variables. The data is taken from the late season at the high-elevation site at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 20 in each analysis.

Parameters	*Dryas octopetala*			*Bistorta vivipara*		
	Parameter estimate	F-Ratio	P-value	Parameter estimate	F-Ratio	P-value
Treatment	-7.11	3.97	0.063	-0.24	12.49	0.003
Cover (%)	0.22	2.52	0.131	0.09	0.32	0.581
Treatment *Cover (%)	-0.27	3.79	0.069	-0.03	0.05	0.832

The relative amount of feeding damage of *Dryas octopetala* and *Bistorta vivipara* showed significantly more damage in the OTCs than in controls (Fig. 6).
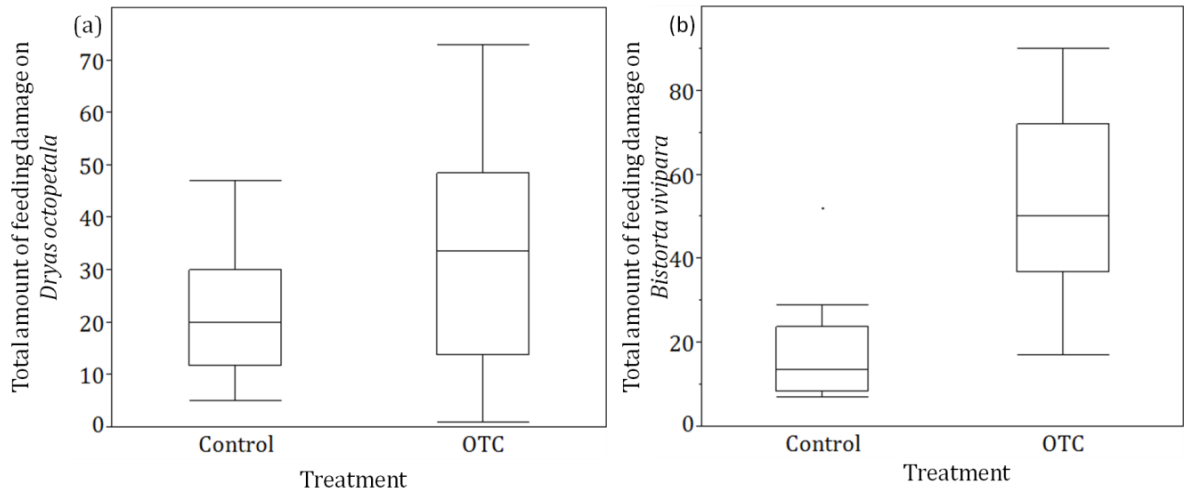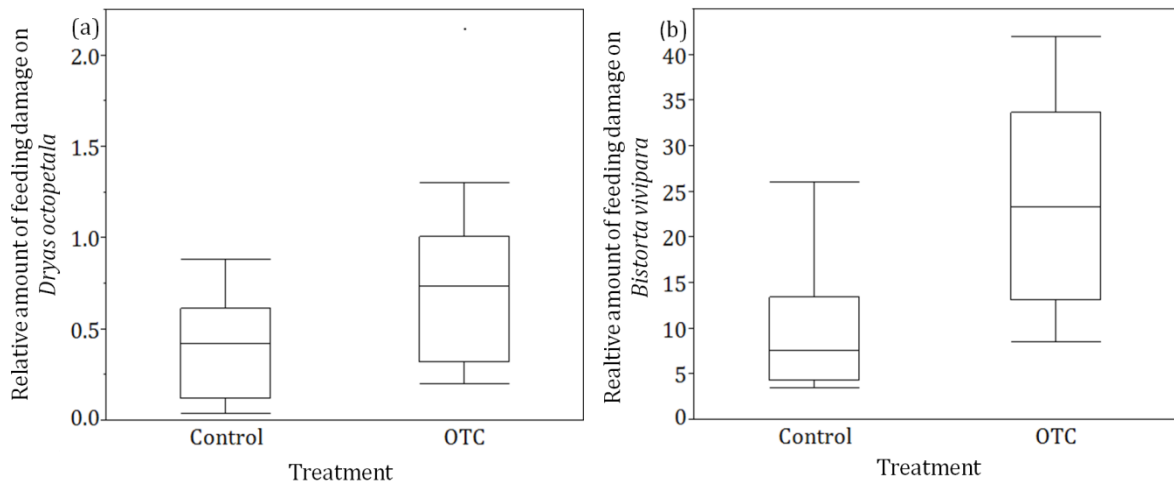

Fig. 6. Box-plots showing median of the relative amount of feeding damage of (a) *Dryas octopetala* and (b) *Bistorta vivipara* in control and OTC for the late season at the high site at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 10 in each plot. Note the differences in scale at the y-axis.

There was a significant relationship between *Zygaena exulans* and the relative amount of feeding damage on *Bistorta vivipara* (Table 3), suggesting an increased damage on *Bistorta vivipara* with increasing number of *Zygaena exulans* independent on the coverage of the plant.

There was no effect of the total number of Lepidoptera larvae.

Table 3. GLM analyses of the relative amount of feeding damage (calculated as the total amount of feeding damage divided by the cover of the plant species) of *Dryas octopetala* and *Bistorta vivipara* with treatment (control, OTC), total number of *Zygaena exulans* and total number of Lepidoptera as explanatory variables. The data is taken from the late season at the high-elevation site at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 20 in each analysis.

Parameters	*Dryas octopetala*		*Bistorta vivipara*	
	Parameter estimate	P -value	Parameter estimate	P-value
Treatment	-0.21	0.040	-0.26	<0.001
Zygaena exulans	-0.30	0.345	-0.44	0.027
Lepidoptera	-0.22	0.574	0.12	0.600

Does experimental warming affect the number of insect herbivores?

The number of *Zygaena exulans* and the number of Lepidoptera (not significant) was highest in the early season (Table 4, Table 5, Appendix 2). In addition, there was a significant difference between controls and OTCs (Table 5), with fewer larvae of *Zygaena exulans* in the controls than the OTCs (Table 4, Appendix 2). Additionally, there was a significant interaction between site and treatment for the total number of Lepidoptera (Table 5), with more larvae in the OTCs in the high site, but no difference in the low site (Fig. 7, Appendix 2).
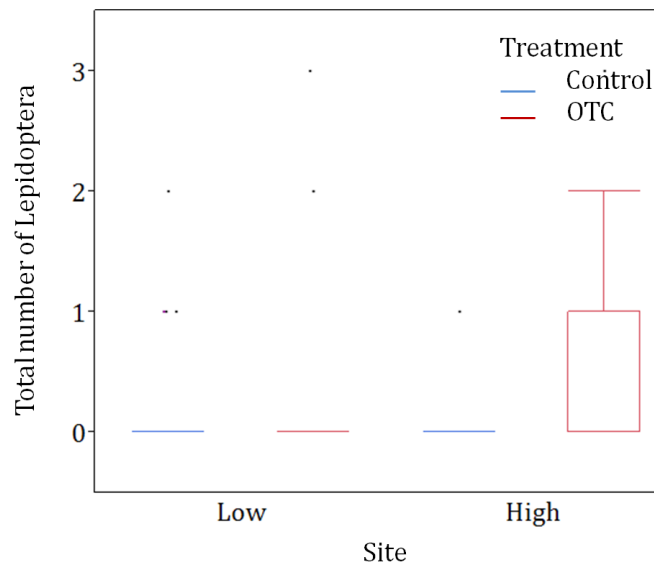

Fig. 7. Box-plots showing median of the total number of Lepidoptera and the interaction between site (low, high) and treatments (control, OTC) at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 20 in each plot. Note the changed color-legend.

There was no effect of site or interaction between season and treatment in the total number of *Zygaena exulans* or Lepidoptera. Furthermore, season, treatment and interaction between season and site were not significant for the total number of Lepidoptera.

Table 4. Total number of *Zygaena exulans* and the total number of Lepidoptera for all data collected at the two study sites at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 80 plots in total.

| | *Zygaena exulans* | | | | All Lepidoptera | | | |
| | early | | late | | early | | late | |
	low	high	low	high	low	high	low	high
Control plots	3	1	0	0	3	1	1	0
OTCs	5	6	0	2	5	6	0	3

Table 5. GLM analyses of the total number of *Zygaena exulans* and total number of Lepidoptera with treatment (control, OTC), season (early, late), site (low, high) and their interactions as explanatory variables at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 80 in each analysis.

| Parameters | *Zygaena exulans* | | | All Lepidoptera | | |
	Parameter Estimate	L-R Chi Square	P-value	Parameter Estimate	L-R Chi Square	P-value
Season	4.66	10.91	0.001	0.40	2.37	0.124
Site				0.11	0.12	0.730
Treatment	-4.31	4.68	0.031	-0.49	2.68	0.102
Season*Treatment	3.81	1.15	0.283	-0.26	0.66	0.416
Site*Treatment				0.65	5.13	0.024
Season*Site				0.33	1.27	0.260

Insect species collected by pitfalls

The insect identification of the pitfall traps (Table 6) showed that no herbivores other than Lepidoptera were recorded in high numbers in any of the sites. *Zygaena exulans* appeared to be the most abundant herbivore species, but only in early/mid-season, while other Lepidoptera larvae than *Zygaena exulans* were found late in the season.

Table 6. Numbers of leaf-feeding herbivores trapped in five pitfall traps at the low- and high-elevation sites at Mt. Sandalsnuten, Finse, Norway during three periods in the summer 2012.

	03.07.2012		28.07.2012		11.08.2012	
	Low	High	Low	High	Low	High
Macro-Lepidoptera Adults						
Erebia pandrose	2		4	5	2	5
Sympistis nigrita						1
Noctuoidea				3	1	
Micro-Lepidoptera Adults						
Tortricoidea			1	3	1	1
Macro-Lepidoptera Larvae						
Zygaena exulans	7	6		11		
Unknown species	2		3	7	2	6
Coleoptera, Chrysomelidae						
Melasoma collaris	1					
Total	**12**	**6**	**8**	**29**	**6**	**13**

4 DISCUSSION

Experimental warming increased the amount of insect herbivory in an alpine *Dryas octopetala* heath at Finse

The results from Finse are in line with previous findings of Roy and colleagues (2004) who found that experimental warming increased herbivory of chewing insect herbivores in a montane meadow on the Rocky Mountains. Kozlov and coworkers (2008) reported the same conclusion based on studies of insect herbivory along geographical gradients in Fennoscandia, showing that herbivory by leaf-chewing and leaf-mining insects increased with temperature rise. Even studies of fossil leaves from the Paleocene-Eocene Warming are in accordance with the results from Finse, concluding that temperature rise increased leaf damage (Wilf & Labandeira 1999).

The increase in insect herbivory might be caused by several mechanisms.

(1) Warming may increase leaf consumption of insect herbivores since warmer temperature may affect the insect metabolism directly (Ipekdal & Çağlar 2012; Kingsolver & Woods 1998; Niziolek et al. 2013).

(2) Warming may increase the abundance of insect herbivores since warmer temperature may improve their reproductive success plus the number (Bale et al. 2002; DeLucia et al. 2012; Dollery et al. 2006; Harrington et al. 2001), assuming the more insects the more feeding damage to plants (DeLucia et al. 2012).

(3) Warming may increase the occurrence and abundance of natural enemies such as parasitoids and pathogens, competitors or predators, affecting insect herbivory indirectly (Ayres & Lombardero 2000; Roy et al. 2004).

(4) Warming may alter leaf suitability to some insect herbivores due to changes in the leaf chemistry, such as the production of antiherbivory compounds (secondary plant metabolites) as a defense mechanism against insect herbivory (DeLucia et al. 2012). Additionally, the seasonal variation in leaf nutrients and alleochemicals in plants should be considered, since that may also drive the amount of feeding (Schoonhoven et al. 2005).

(5) Warming may change food preference of insect herbivores Ipekdal & Çağlar 2012; Schoonhoven et al. 2005). However, it is not known what drives that mechanism, but changes in the insect's behavior and/or changes in the chemical composition of the plant, may be responsible (Schoonhoven et al. 2005).

Amount of insect herbivory varied between plant species

The results from Finse showed that the amount of herbivory varied between plant species, with more feeding damage on *Dryas octopetala* and *Bistorta vivipara* than on the others. This is in line with the findings of Roy and colleagues (2004), who showed that the amount of herbivory varied among plant species.

The species cover per plot could explain the difference in the amount of feeding damage, because only feeding damage on *Dryas octopetala* increased with cover. In fact, the *Dryas octopetala* cover (5-90 %) varied much more than that one of *Bistorta vivipara* (2-4 %), which may explain the result. Nevertheless, a similar result could be assumed considering a greater variation in *Bistorta vivipara* cover since Hasle (2013) showed that the increase in feeding damage on that species was probably due to a greater cover of that species in the OTCs. On the other hand, Hasle (2013) stated that the increase in feeding damage on *Dryas octopetala* at the low-elevation site was due to higher herbivore pressure in the OTCs. However, my analysis suggests a combination of increased cover and increased feeding independent of cover as possible explanation to the increase in feeding damage on *Dryas octopetala*.

The fife mechanisms mentioned in the section above, might give species-specific preferences and therefore might explain the different responses between species.

Niziolek and coworkers (2013) found that the chewing Japanese beetle *Popillia japonica* Newman increased leaf consumption on soybean with elevated temperature. In contrast, Johns and colleagues (2003) did not show such an increase in their study on the beetles *Octotoma championi* and *O. scabripennis*. Thus, not every insect herbivore increase consumption with warming, and the effect is likely to be species-specific (Bale et al. 2002). This may explain the increased feeding damage on *Dryas octopetala* and *Bistorta vivipara* and not the others in OTCs, assuming increased leaf consumption of insect herbivores feeding on those plant species. However, to my knowledge, there has not been done such a study at Mt. Sandalsnuten.

The literature stated in the previous section, that natural enemies may increase under warmer conditions, may explain the increased feeding damage on *Dryas octopetala* and *Bistorta vivipara*, assuming that insect herbivores preferring those plant species would experience a lower pressure of natural enemies or predators inside the OTCs, as opposed to insect herbivores preferring other plant species. To my knowledge, this has not been studied for the fauna at Mt. Sandalsnuten; however it would be of interest to know which natural enemies or predators may

regulate the abundance of insect herbivores, which again cause feeding damage in the vegetation.

Nybakken and colleagues (2008) showed that experimental warming at Mt. Sandalsnuten affected very little the concentration of carbon-based secondary compounds (CBSCs) in *Dryas octopetala*, *Bistorta vivipara* and *Salix reticulata*. This suggest, that the concentration of CBSCs does not explain the different responses between species, rather the decrease in other antiherbivory compounds might have caused the increased feeding damage on *Dryas octopetala* and *Bistorta vivipara.* That change in antiherbivory compounds may even altered the food preference of the insect herbivore (Schoonhoven et al. 2005).

Which species do cause the feeding damage?

Most of the feeding damage I have seen in the field looked similar to that in the feeding preference experiment with *Zygaena exulans,* I carried out in cooperation with T. Hasle (Hasle 2013). Leaves of all studied plant species, both in the field and in the lab experiment, were either fed on the edge, in the middle or on the surface.

During my field work, I was not able to determine which feeding damage was made by which insect herbivore; the same applies to the collected data at the low site (Hasle 2013). For that reason, it is difficult to identify which insect species caused the increased herbivory under experimental warming.

Zygaena exulans was the most abundant insect herbivore during the early season in the pitfalls and in the OTCs, suggesting this species cause most of the feeding damage at that time. However, it is also possible that feeding by *Zygaena exulans* could have continued after the first registration in the early season and represent much of the increased feeding damage later in the season.

The results from the pitfall traps, which match earlier studies as reported in materials and methods, indicated that there were other insect herbivores within the study area,

than those considered in my analysis. Those other insect herbivores might have caused some of the recorded feeding damage and may explain the increased herbivory early and late in the season particularly.

The pitfall traps indicated for example the adult macro-Lepidoptera *Sympistis nigrita* as potential insect herbivore at Mt. Sandalsnuten, considering its monophagous larva feeding only on leaves of *Dryas octopetala* early in the season (Lepidoptera.no 2013). The results from the pitfalls showed high numbers of the adult macro-Lepidoptera *Erebia pandrose*, particularly in mid- and late season, suggesting larval feeding in the beginning of the season (Lepidoptera.no 2013). *Erebia pandrose* is a specialist mono- or oligophagous herbivore, feeding only on *Festuca*, *Poa* and *Sesleria* species, which belong to the same plant family. The adult micro-Lepidoptera *Tortricoidea* was identified as a potential insect herbivore by the pitfall traps in mid- and late season which is consistent with my findings in the field. *Tortricoidea* may feed during the whole growing season until the onset of hibernation (Crook 1951). The adult macro-Lepidoptera *Noctuoidea* was identified in the pitfall traps in mid-and late season. Plus I recorded one larva of *Noctuoidea* early in the season. Combing both findings, it can be assumed that larvae of *Noctuoidea* might contribute to feeding damage in the early season. The leaf beetle *Melasoma collaris* L. (Chrysomelidae) could have also caused feeding damage within the vegetation, particularly on green leaves of its preferred host plant *Salix herbacea* (Hågvar 1975) early in the season. The pitfall traps showed high numbers in abundance of an unknown larva of a Macro-Lepidoptera, particularly late in the season, which might be either of the above mentioned Lepidoptera species.

What plant species do *Zygaena exulans* prefer?

The larva of *Zygaena exulans* is considered a generalist polyphagous herbivore(Naumann et al. 1999 cited in Diecker et al. 2011), thus feeding on more than one host plant species and even family (Lepidoptera.no 2013). This is in line with the preference feeding experiment (Hasle 2013), which showed that *Z. exulans* fed on *Dryas octopetala*, *Bistorta vivipara*, *Salix reticulta* and *S. herbacea* without having any

particular preference (Hasle 2013). This is in contrast to the preference test conducted by Hågvar (1976), showing that *Z. exulans* liked mostly *Salix herbacea.*

My recordings in the field, showed more feeding damage on *Dryas octopetala and Bistorta vivipara* than on *Salix reticulta and Salix herbacea.* Assuming that *Z. exulans* is the major insect herbivore responsible for these feeding damage, this clearly differs from the preference test. However, it could be also that *Z. exulans* feed on the most abundant plant species, which was *Dryas octopetala*, supporting the findings of Wilf and Labandeira (1999), that herbivory was higher on the most abundant plant group in the vegetation.

Differences in feeding preferences between lab and field may be explained with the fact, that insect herbivores meet a more heterogeneously spectrum of plant diversity respectively stimuli (e.g. odor and color) and deterrents in the field, than it is possible to establish within a lab experiment (Schoonhoven et al. 2005). Stimuli to choose and to start feeding including three phases: volatile and visual plant cues and non-volatile plant chemicals (Finch & Collier 2000).

However, to my knowledge, there has been no study about which stimulants drive *Zygaena exulans* feeding on the above mentioned plant species in the field.

Number of *Zygaena exulans* larvae increased within experimental warming

Warmer temperatures can speed up insect development and reproduction potential (Ayres 1993; Ayres & Lombardero 2000; DeLucia et al. 2012; Harrington et al. 2001; Malmström & Raffa 2000) due to a prolonged plant growing season allowing for more insect generations within a season, and thus a shorter time for life-cycle completion.

Studies of Dollery and colleagues (2006) reported variable results among species groups, mites tended to increase in OTCs while Symphyta larvae and weevils decreased under experimental warming in a *Dryas* heath in West Spitsbergen. Liu and coworkers (2011) showed that the abundance of the noctuid moth *Melanchra pisi*

increased by a factor of 10 in a Tibetan meadow. Adler and colleagues (2007) again showed that experimental warming did not increase the abundance of aphid *Obtusicauda coweni* in a montane meadow in the Rocky Mountains. The results from Finse differed between *Z. exulans* and all Lepidoptera larvae. Thus, species-specific responses might also be found here.

The number of *Z. exulans* increased in OTCs, which is in line with the general predicted response of insect herbivores to warming (Bale et al. 2002; Harrington et al. 2001). The number of *Z. exulans* increased within the OTCs, but not in the area in general, as the species might only spend part of their life within the OTCs. *Z. exulans* might only feed inside the OTCs due to favorable microclimate such as higher temperature, but hibernate/mate outside the OTCs. The species might be able to respond to higher temperatures than found normally at Mt. Sandalsnuten, since they live under much warmer conditions in southern Europe (Dieker et al. 2011).

The larval abundance of *Z. exulans* was highest early in the season. This may be explained with the life cycle of *Z. exulans*, which takes at least two years (Hågvar 1976). The larvae may concentrate its feeding early in the season before pupation (Dieker et al. 2011), or before possible larval diapauses.

However, the number of insect herbivores, for both *Z. exulans* and all Lepidoptera larvae, observed and used in the analysis was very low and for that reason, these results might be interpreted with care.

Site did not affect the amount of insect herbivory

I expected more insect herbivory at the lower site due to higher temperatures, but my analysis did not show any difference between the two sites.

This might be caused by an earlier snowmelt and thus longer growing season at the higher site (Nybakken et al. 2011) which may neutralized the temperature effect and so the difference in temperature between the low- and high site. However, this is not

consistent with the general trend, that the date of snowmelt may predict the amount of insect herbivory (Roy et al. 2004). This suggests that plants at warmer temperatures and earlier snowmelt receive more damage, since the insects find food available there sooner (Roy et al. 2004).

Additionally, the results from Finse showed that the abundance of Lepidoptera larvae was positively affected by the combination of temperature rise and a higher elevation. I suppose that the Lepidoptera larvae simply moved to the warmer OTCs that melted out first because of less wind exposure.

5 CONCLUSIONS

To conclude, this study points out that climate warming can affect insect herbivory in the alpine *Dryas* heath at Finse. Warming increased the amount of insect herbivory on a plot scale and varied between plant species, showing that some plant species such as *Dryas octopetala* and *Bistorta vivipara*, are more susceptible than others. Concluding that insect herbivory may have important impact on species composition and ecosystem functions.

More research is needed to explain the different responses of plant species to warming. Future research should include measurements of nutrient concentration to find out what kind of nutritional value in the leaf do insect herbivores prefer. That should be considered under field conditions as well as in lab experiments. This may answer why insect herbivory varied between plant species, plus, it will tell more about the food-plant preference of insect herbivores generally, and *Zygaena exulans* particularly.

However, the consideration of other environmental factors, apart from temperature, such as CO_2, UVB-levels, precipitation, and their combination in long-term studies within alpine and arctic ecosystems, shall be from interest for future climate change research upon insect herbivory.

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Appendix 1

Overview of all recorded feeding damage on the different plant species in controls and OTCs at the low-and high-elevation site during the early- and the late season at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 80 plots in total. Denote missing numbers.

	Early				Late			
	Low		High		Low		High	
	Control	OTC	Control	OTC	Control	OTC	Control	OTC
Bistora vivipara	174	164	86	489	116	216	179	535
Carx	2				3	13		1
Dryas octopetala	247	212	168	225	325	786	219	335
Parnasia palustris						7		
Poa alpina							2	
Rannuculus acris							2	
Salix herbacea			9				25	3
Salix reticulata	7	6	15	12	13	16	61	5
Saussurea alpina	4	3		6	7	5	7	4
Thalictrum alpinum						3		
Tofildia pusilla	2				11	4		
Vaccinium uliginosum		1			9			
Total	**436**	**386**	**278**	**732**	**484**	**1050**	**495**	**883**

Appendix 2

Overview of all recorded insects in controls and OTCs at the low-and high-elevation site during the early- and the late season at Mt. Sandalsnuten, Finse, Norway summer 2012. n = 80 plots in total. Denote missing numbers.

	Early				Late			
	Low		High		Low		High	
	Control	OTC	Control	OTC	Control	OTC	Control	OTC
Amara Alpina	2	2		3				1
Byrrhidae		2		1		1		
Curculionidae (adult)				1				
Geometridae (larva)								1
Lepidoptera						1		
Lepidoptera or Sawfly					1			
Most likely predator								1
Noctuoidea (larva)					1			
Tortricidae (adult)					1			
Unknown caterpillar								1
Zygaena exulans (larva)	3	5	1	6				2
Zygaena exulans (adult)					1	1	3	3
Total	**5**	**9**	**1**	**11**	**4**	**2**	**3**	**9**