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The survival of moth larvae feeding on different plant species in northern Fennoscandia

5th instar of winter- and autumn moth (Belsing 2015).

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Abstract

Northern Fennoscandia belongs to the sub-arctic environment and its forests are mostly composed of mountain birch trees (*Betula pubescens* ssp. *czerepanovii*). Outbreaks by autumn moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) are one of the most important natural disturbance factors in the mountain birch forests, with important implications for future ecosystem functioning. If there will be a vegetation shift due to climate change or greater infestation and competition between different moth species, the moth larvae will have to feed more on alternative plant species. However, the ability of these species to feed, grow and survive on these alternative food sources is poorly understood.

The aim of this study was to see if the pupae weight, the frass (excrement) amount and the survival rate differed for the autumn- and winter moth in Northern Fennoscandia, depending on which type of leaves the larvae feed on. The plant species chosen was the preferred food source mountain birch and two possible alternative food species; dwarf birch (*Betula nana*) and bilberry (*Vaccinium myrtillus*). The study area was around Tromsø in northern Norway. The larvae and leaves were picked at random locations around Tromsø and the autumn- and winter moth larvae were separated into different containers containing each of the three plant species. A total of 33 containers were set-up with 20 larvae and 7g of fresh leaves in each. Leaves were changed every fourth day, where old leaves were removed and the frass were swept up. At the end of the experiment, the remaining larvae and the pupae were counted, and then together with the frass dried at 60°C for 48h to get the dry weight.

A comparison between the two moth species showed that there was a significant difference in the pupae weight, but none in the frass amount and survival rate. The autumn moth’s pupae weight and frass amount did not significantly differ between the food sources. The survival rate for autumn moth, when feeding on dwarf birch, was much higher than when feeding on mountain birch or bilberry. The winter moth’s pupae weight did however differ significantly between the food sources. The frass amount and the survival rate between the plant species did not differ, suggesting that the winter moth is a feeding generalist less likely to be limited by food availability.

With a changing climate and potentially more severe outbreaks on the mountain birch forests, the forests might suffer very badly and might not recover in all areas. A different food pattern of the moths with other plant species as hosts might change the nutrient cycle and permit greater impacts of warming than would otherwise occur. A key impact of moth activity in arctic ecosystems will be in regulating available nitrogen under future climate shifts. A greater infestation of moths in these sensitive ecosystems can also alter the already ongoing climate changes and cause vegetation shifts. The winter moth has also over the past years expanded more and more into the autumn moths' domain, but the autumn moth has also started to occur even in the coldest most continental regions. The moth species possible ability to easily change the main food source when another is unavailable, e.g. damaged from outbreaks, cause a more direct threat to the arctic vegetation. Further work in this area is required to advance the understanding of the underlying factors driving these interactions.

Keywords: Autumn moth, winter moth, northern Fennoscandia, outbreaks and sub-arctic environment.

Sammanfattning

Norra Fennoskandia tillhör den subarktiska miljön och skogarna består främst av fjällbjörk (*Betula pubescens* ssp. *czerepanovii*). Dessa skogar utsätts periodvis för avlövning på grund av utbrott av fjällbjörkmätare (*Epirrita autumnata*) och allmän frostfjäril (*Operophtera brumata*). Utbrott av mallarver är en av den största och viktigaste naturliga störningen på fjällbjörkskogarna och med klimatförändringarna kommer ekosystemfunktionerna att påverkas. Om det sker en vegetationsförändring på grund av klimatförändringar, eller fler angrepp och mer konkurrens mellan olika malarten, kommer malens larver vara tvungna att livnära sig mer på alternativ föda till fjällbjörken. Mallarvernas förmåga att äta, växa och överleva på alternativ föda är därför viktig att förstå.

Syftet med den här studien var därför att se om puppavikten, mängden frass (exkrement) och överlevnadsgraden för fjällbjörkmätaren och den allmänna frostfjärilen i norra Fennoskandia skiljer sig beroende på vilka växtarter de får livnära sig på. De valda växtarterna för studien var den föredragna fjällbjörken och två alternativa växtarter; dvärgbjörk (*Betula nana*) och blåbär (*Vaccinium myrtillus*). Studieområdet var belagt i Tromsö, Nordnorge. Larver och löv plockades slumpmässigt runt om Tromsö och de två malarterna separerades i olika behållare innehållande de tre olika växarterna. Totalt 33 behållare användes, innehållandes 20 larver med 7g färska löv i varje. Var fjärde dag byttes de gamla löven ut mot nya och allt frass togs omhand. Vid slutet av experimentet räknades pupporna och de kvarvarande larverna, för att sedan tillsammans med frassen torkas i 60° i 48h för att få ut torrvikten.

Först jämfördes de två malarterna mot varandra och det visade sig vara en signifikant skillnad i puppavikt mellan dem båda. Det var däremot ingen skillnad i mängden frass eller överlevnadsgraden. Fjällbjörkmätarens puppavikt eller mängden frass skilde sig inte signifikant mellan de olika födoalternativen. Däremot var överlevnadsgraden för fjällbjörkmätaren större vid en diet av dvärgbjörk än av fjällbjörk och blåbär. Den allmänna frostfjärilens puppavikt skiljde sig däremot signifikant mellan de olika födoalternativen. Det gjorde däremot inte mängden frass eller överlevnadsgraden, vilket kan betyda att den allmänna frostfjärilen inte begränsas lika lätt i sitt födosökande.

Ett föränderligt klimat och fler utbrott av mallarver på fjällbjörkskogarna kommer resultera i att skogarna drabbas negativt. Eventuellt kommer de inte alls att kunna återhämta sig i vissa områden. Ett annat födomönster med andra växarter som huvudföda kan förändra näringscykeln och resultera i kraftigare uppvärmning av klimatet än vad som annars skulle ske. En viktig effekt av malaktiviteten i de arktiska ekosystemen kommer att vara att reglera tillgängligt kväve vid framtida klimatförändringar. Fler och kraftfullare malangrepp i dessa känsliga ekosystem kan också förändra den pågående klimatförändringen och orsaka vegetationsförändringar. Den allmänna frostfjärilen har också sedan några år tillbaka börjat sprida sig mer och mer inpå fjällbjörkmätarens territorium, medan fjällbjörkmätaren har flyttat till kallare mer kontinentala områden. Malarnas potentiella förmåga att obehindrat kunna byta ut sin huvudföda när den inte är tillgänglig, exempelvis på grund av skador från tidigare malutbrott, kan orsaka ett mer direkt hot mot den arktiska vegetationen. Ytterligare undersökningar inom det här området krävs för att förstå de bakomliggande faktorerna som driver de här interaktionerna.

Nyckelord: Fjällbjörkmätare, allmän frostfjäril, norra Fennoskandia, utbrott och subarktiska miljöer.

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1. Introduction

1.1 Northern Fennoscandian forest extent and status

Northern Fennoscandian forests are mostly composed of mountain birch trees (*Betula pubescens* ssp. *czerepanovii*) that experience periodic defoliation due to outbreaks of autumn moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) (Young et al. 2014). Autumn moth is the original occupant in the northern Fennoscandian forests but the winter moth has since the last 100 years succeeded in creating a stable population (Amundsen and Lie 2014). Depending on the size of the larvae population the defoliation extent will vary. Only minor foliage damage is expected when the population is small, whereas during an extensive outbreak the larvae might cause complete and widespread defoliation, where it can take years before the trees are fully recovered (Tuomi et al. 1989; Vindstad et al. 2011). An important consequence of the outbreaks is that they change the resource availability for many consumer species (Vindstad et al. 2014). A high grazing pressure by larger herbivores like reindeers (*Rangifer tarandus*) in the damaged areas can also shift the vegetation from mountain birch forests to tundra (Karlsen et al. 2013). The cascading effects of larvae outbreaks on the mountain birch forest ecosystems will likely depend on the initial state of the forest, and the effects will have impacts on the food web (Jepsen et al. 2013). Rodents and saproxylic beetles are for example affected positively after an outbreak since e.g. the beetles are dependent on dead or dying wood (Vindstad et al. 2014).

With the climate change, arctic ecosystem functioning will be affected. These ecosystems are vulnerable to climate change and its impact. Disturbances such as insect outbreaks and forest fires are very likely to increase in frequency and severity, as a facilitation of non-native species that will inhabit the arctic environment (ACIA 2004). It is still however, unclear how the insect outbreaks in Fennoscandia affect ecosystem functioning, since the defoliation does not immediately kill the host tree (Jepsen et al. 2013). Larvae abundance and so the defoliation are more severe close to the tree line and therefore the effects on the forest are much greater than on lower altitudes (Schott et al. 2013). This is very clear in the coastal region of northern Norway where the larvae outbreaks almost always occur near or at the altitudinal tree line (Vindstad et al. 2011). Where the terrain is more varied (as in the coastal districts of north-western Fennoscandia) the outbreaks can be very local, while for a more topographically homogenous terrain (interior and coastal eastern parts of northern Fennoscandia) the outbreaks may extend over hundreds of square kilometres (Schott et al. 2013).

Outbreaks by moth larvae are one of the most important natural disturbance factors in the mountain birch forests. By consuming most leaves in the forest they can change the living conditions for many other plant- and animal species (Amundsen and Lie 2014). The forests have experienced occasional large outbreaks for a long time, which is documented as far back as historical records go, since 1860 (Tenow 1972). Hence the resilience to the outbreaks should be high, but since these environments are very climate sensitive the outbreak severity has increased with the warming climate (Karlsen et al. 2013). These northern forests are important ecosystems, but their future under changes in climate and herbivore pressure still remains relatively poorly understood compared to other global biomes. If there will be a vegetation shift due to either climate change or greater infestation and competition between the different moth species, the moth larvae will have to feed more on alternative plant species. However, the ability of these species to feed, grow and survive on these alternative food sources is poorly understood. Understanding the ecosystem impacts of these moth species requires improved understanding of their life cycle and food preference.

1.2 Insect herbivores general role and effects on nutrient cycling

During the larvae cycle the amount of larvae can go from being barely detectable to several hundred per branch during a severe outbreak. During outbreaks the larvae does not only feed on mountain birch leaves but have to graze on common and available deciduous understory species like dwarf birch (*Betula nana*), bilberry (*Vaccinium myrtillus*) and northern bilberry (*Vaccinium uliginosum*) (Karlsen et al. 2013). The larvae also feed on other plant species like willow (*Salix caprea* & *Salix lapponum*) and rowan (*Sorbus aucuparia*) when they can find it (Jepsen Personal communication). However, the moth larvae’s possible grazing on plant species that do not create the majority of the vegetation, or human introduced plant species, is not in an immediate threat to suffer from complete and widespread defoliation. The understanding and knowledge of the moth larvae’s grazing on understory species is not as well studied as for mountain birch.

It is also possible for large amounts of larvae to dramatically change the conditions for the understory plant species, but not necessarily by direct defoliation. There will be a change in light conditions since the canopy is reduced, added nutrients from larvae excrement (called frass) and more decomposed carcasses, an altered recycling of nutrients and reduced root competition (Karlsen et al. 2013).

Invertebrates are the largest and most species rich group of herbivores globally and their outbreaks are likely to affect the resource dynamics in subarctic environments (Kaukonen et al. 2012). The key nutrients controlling plant growth are nitrogen and phosphorus, but the input from herbivores is poorly understood (Hartley and Jones 2004). Moth herbivory may provide a shortcut for nutrient and carbon input to subarctic soils, mostly in the form of partly eaten leaves, carcasses and frass (Kaukonen et al. 2012). Herbivores reduce the nitrogen and phosphorus preserved by plants through removal of nutrient-rich green leaves, which is eventually transferred to the soil. The herbivores can thereby alter the amount and types of organic matter that reach the soil (Wardle et al. 2004). Increased soil nutrients suggest enhanced resource turnover in mountain birch forests due to outbreaks of moth larvae (Kaukonen et al. 2012). So insect herbivores are potentially important but their impacts on forest nutrient cycling are relatively poorly understood compared to larger animals' in short statured vegetation.

1.3 Moth herbivores in northern Fennoscandian forests and traits of food species

The leaves within a single tree can differ in quality and therefore affect the growth, reproductive capacity and survival for the leaf herbivore, for example the moth larvae. The variations can be due to intrinsic sources e.g. different age of the leaves or size difference, or to extrinsic sources e.g. light conditions or damage-induced responses (Suomela et al. 1995). It has even been shown that the best leaf quality on birch trees are on north-facing leaves. The reason for this is not fully understood though (Suomela et al. 1995). Leaves also use chemical traits against herbivores. Depending on plant species, the leaf chemistry will differ and thus determine if the leaves will be hard to digest or not (Lempa et al. 2004; Ruuhola et al. 2013). Leaves that sprout from defoliated trees or trees from warm environments contain less water than leaves from intact trees or from cold environments (Huttunen et al. 2013). All of this will have an impact on the herbivorous insects efficiency of utilizing available nutrients in the leaves, especially since lower water content is linked to higher leaf toughness (Huttunen et al. 2013). It has also been shown that, depending on the type of plant species the moth larvae feed on, the pupation time differs. For example, when feeding on alternative understory species, the development time to pupae is longer and the pupae weigh less than when feeding on the main host, mountain birch (Yang et al. 2008).

2. Aim and study questions

The overall question motivating this project is if the different species of moth larvae will survive and grow sufficiently when only feeding on plant leaves other than their preferred food source, mountain birch. Depending on how they cope with non-preferred food sources, they may have a different impact on the ecosystem functioning in the future. To address this aim, larvae were fed different plant species to see if there is a difference in the pupae weight, the frass amount and how many larvae that turns into pupae. The focus was on the plant species mountain birch, which is the main food source, and dwarf birch and bilberry which are two common understory species. The moth species, autumn- and winter moth, were the study organisms. The study site was around Tromsø in northern Norway where the forest type is coastal mountain birch.

The following questions are identified:

> **Question 1. Food preference:** If the larvae only get to feed on understory species, will their pupae weight be lesser than when feeding on their preferred food mountain birch?
>
> **Question 2. Digestibility:** Depending on the type of food, will one generate more frass and thereby add more nutrients to the ground? Will a leaf that is considered harder to digest and less nutritious produce more or less frass?
>
> **Question 3. Survival:** Which food source will result in the most optimal growth and survival of the moth larvae? Which moth species will be able to adapt to the food given more easily?

3. Background

3.1 Sub-arctic environment

The northern Fennoscandian region with mountain birch forests belongs to the sub-arctic environment and is characterized by a climate with both oceanic and continental elements. This vegetation type occurs almost solely in Fennoscandia with northern Norway as the midpoint (Young et al. 2014). With warmer temperatures, the arctic environment is facing a greening effect (more plant species can inhabit and survive in the area), but this is not entirely the case for the sub-arctic (Amundsen and Lie 2014). The sub-arctic is instead facing three threats: intense infestation of moths, more forest fires and an elevated drought pressure that will instead cause a browning effect (less vegetated and barer soil) (ACIA 2004; Amundsen and Lie 2014). This has already been seen for some parts of northern Norway. However, Huttunen et al. (2013) state that with increased summer temperatures, plant functions may become modified. Irrespective of defoliation level the amount of sprouting leaves and the timing of leaf burst is unaffected in recently damaged trees. This is unexpected since earlier studies e.g. by Tuomi et al. (1989) showed very negative impacts on the mountain birch after severe defoliation with the emergence of new foliage. However, if warmer summers result in more growing degree days, that will result in earlier leaf burst and an increased leaf area index and light interception that may mitigate the effects of defoliation (Huttunen et al. 2013).

3.2 Mountain birch

Picture 1: Mountain birch forest (Belsing 2015).

Mountain birch (*Betula pubescens* ssp. *czerepanovii*) is a northern European deciduous hardwood species that forms the arctic tree line in northern Fennoscandia (Picture 1) (Lempa et al. 2004). They are monoecious, which means they have both male and female flowers (called catkins) that blossom differently and are wind pollinated (Picture 2) (Klemola et al. 2010). The number of catkins vary from year to year and strongly depend on the weather in the year prior to flowering, since the initiation of flower buds takes place in the late summer that precedes the year when flowers mature (Klemola et al. 2010). The mountain birch leaves also go through large chemical changes with leaf unfolding and maturation in the foliage (Lempa et al. 2004). When the leaves are still buds they require energy for enlargement. The young leaves cannot photosynthesize enough to support their own growth, which is common in cold environments. So during the early days of foliar expansion in spring, the buds are dependent on the root carbohydrate reserves (Huttunen et al. 2013). The energy source that is required for leaf and fine root growth is starch that is stored in the bark and coarse roots (Huttunen et al. 2013).

The energy transport system is based on the sap flow and stored reserves have often been compromised after insect outbreaks. This can be seen the following spring by delayed bud burst, reduced height and decreased production of reproductive organs, male and female catkins (Huttunen et al. 2013). Weakly developed meristems will be unable to take up enough carbon and nutrients to fill the common storage compartments of the tree. It may be this low uptake strength, and not necessarily a shortage of nutrients, that prevents the leaves from getting enough nutrients which in turn results in the delayed bud burst (Ruohomäki et al. 1996). The birch leaf quality, as a nutritious food resource for herbivores, also decreases as summer continues and during periods of extreme warm spring temperatures the birch leaves deteriorate very rapidly, in one week or even less (Suomela et al. 1995).

The leaves (Picture 2) have both physical (e.g. leaf toughness) and chemical traits that can act as defence against herbivores, mostly insects (Lempa et al. 2004). They can change the nutrient quality of intact leaves close to leaves that have been damaged, possibly as a defensive response to herbivores. It also seems that the birch leaves that are usually preferred by the insect herbivores have the highest potential for successful recovery after herbivore damage (Lempa et al. 2004). Dense mountain birch forests also survive a larvae outbreak much better than sparse ones. Sparse birch forests grow in nutrient poor locations and defoliation in these forests cause extensive changes in ground vegetation (Amundsen and Lie 2014). The large amount of larvae during an outbreak will result in a lot of frass and dead larvae that will fall to the ground and work as fertilizer to then promote the growth of graminoids (grasses) over ericaceous dwarf shrub (heath). The process is strengthened further when more sunlight reaches the ground when the leaves are gone (Amundsen and Lie 2014). Recent results show that in areas after a severe larvae outbreak, the understory vegetation had shifted completely from ericaceous dwarf shrub to graminoid dominance (Jepsen et al. 2013).


Picture 2: Mountain birch leaves (above) & male catkin (below) (Belsing 2015).

3.3 Understory species

3.3.1 Dwarf Birch

The dwarf birch (*Betula nana*) (Picture 3) is a prostrate shrub with many trunks and a common species in the sub-arctic environment. It is a low shrub (0.2 – 0.8 m) that grows above the tree line and on heath- and peat lands where it often forms dense stands in swampy areas (Ruuhola et al. 2013). While the mountain birch forms the forest community below the tree line, the dwarf birch is widespread above the tree line (Wilsey et al. 1998). It is well adapted to a northern climate with the optimal temperature of net photosynthesis as low as 13°C (Ruuhola et al. 2013). They are monoecious and wind pollinated, and can hybridize with other birch species (Hanhimäki et al. 1994).

The dwarf birch is considered to be less susceptible to damage from moth larvae but the induced resistance is not as closely studied as for other birch species (Ruuhola et al. 2013). It is also shown that the dwarf birch is a poorer food source than mountain


Picture 3: Dwarf birch leaves (above) & male catkin (below) (Belsing 2015).

birch for the autumn moth (Hanhimäki et al. 1994). The difference in leaf chemistry might explain this, since dwarf birch contains higher total levels of HTs (hydrolysable tannins). Tannins are a broad group of polyphenolic compounds that reduce protein digestion due to reversible hydrogen bonds between tannins and proteins. Due to this bond, the leaves will be hard to digest and will be distasteful to herbivores (Ruuhola et al. 2013).

Studies on dwarf birch in Abisko, northern Sweden, and Toolik Lake, Alaska, show that there are great differences in the amount of tannins. One population in a specific area can contain up to 50% more tannin in the leaves than another population (Graglia et al. 2001. This can be due to differences within the species, sub-species or evolutionary due to different herbivore pressure. Dwarf birches that grow under more nutrient limiting conditions also create more tannins than populations in more nutrient rich areas. A warmer climate will however most likely result in more tannin production for all dwarf birch populations (Graglia et al. 2001). The leaf phenolic compounds can also be altered by environmental fluctuations (Torp et al. 2010).

3.3.2 Bilberry

Bilberry (*Vaccinium myrtillus*) (Picture 4) is a common ericaceous dwarf shrub in Fennoscandia and is a deciduous perennial woody dwarf shrub (Nestby et al. 2011). The plant is an important food source for many species throughout the year (Laine and Henttonen 1987). It grows in mountain birch forests and in the low-alpine area up to 1700 m.a.s.l. but requires the protection of snow during winter (Olsson and Nylén 1985). The plants favour areas of better-drained acid soils. The flowers are initiated and developed on one-year old twigs the year prior to flowering and overwinter in a dormant bud. They flower in May – June and are insect pollinated. The berries are then developed in July – August (Nestby et al. 2011) and produce a large number of seeds (Hegland et al. 2005).


Picture 4: Bilberry leaves and flowers (Belsing 2015)

Bilberry does not appear to use chemical traits like phenolic compounds as a defence mechanism against herbivores to the same extent as dwarf birch, but instead compensates for any leaf tissue lost by utilizing underground reserves (Laine and Henttonen 1987). Phenolics and carbon/nutrient ratios are used as indicators of food quality and phenolic compounds can act as protective agents, natural toxicants against herbivores (Laine and Henttonen 1987). The plant has instead a good ability to respond and compensate for lost tissue due to herbivory as long as it is not too severe. After a high herbivore intensity it takes five years for the plant to fully recover and the plants might have difficulty in competing in this state, which is why graminoids may take over (Hegland et al. 2005).

3.4 Moth species

3.4.1 The Geometridae family

The three moth species presently inhabiting Fennoscandia belong to the family *Geometridae* and they all have a very similar life cycle (Amundsen and Lie 2014). The autumn moth (*Epirrita autumnata*) (Picture 5) is commonly found in continental climates and is the original occupant in Fennoscandia (Young et al. 2014). They have an outbreak cycle of approximately ten years (Amundsen and Lie 2014).

Picture 5: 3rd instar of autumn moth (Belsing 2015)

The winter moth (*Operophtera brumata*) (Picture 6) is found in more maritime climates but has recently been expanding into more continental areas (Young et al. 2014). It is only a century ago that the winter moth started to appear in northern Fennoscandia (Amundsen and Lie 2014) and they have now an outbreak cycle that usually occurs 1 – 2 years after the autumn moth (Young et al. 2014). The continental climate with cold winters and summers limited the spread of winter moth, but the changing climate with warmer temperatures can partially explain the population spreading (Huttunen et al. 2013). It is a serious threat to the forests and understory vegetation to have two moth species that have outbreaks with extreme defoliation so close to each other. This can explain why some forests have had difficulty coping in recent years (Amundsen and Lie 2014).

Picture 6: 3rd instar of winter moth (Belsing 2015)

A new third species of moth, the scarce umber moth (*Agriopis aurantiaria*) (Picture 7), has since the last 15 years invaded the coastal regions of northern Norway. The scarce umber moth has still a smaller population compared to autumn- and winter moth, but is on the way to become a serious threat to the coastal birch forests of Norway (Amundsen and Lie 2014). Due to its lower population it is not following any outbreak cycle yet. The population is scattered and seem to favour rowan leaves (Jepsen Personal communication).

Picture 7: 3rd instar of scarce umber moth (Belsing 2015)

3.4.2 General life cycle

It is of high importance that the moths hatch synchronously with their host plants budburst in order to feed on the young foliage (Vindstad et al. 2011). The moths start their lives as an egg that is laid during autumn on all types of vegetation. The eggs survive over winter and the larvae hatch during spring which coincides with the birch bud burst. The moths egg can tolerate winter temperatures to below $-30°$C, where the autumn moth is the most cold tolerant and can survive down to $-37°$C (Jepsen et al. 2008). The larvae only feed for approximately one month where they go through five instars (development stages) before they pupate in ground litter (Suomela et al. 1995). Their reproductive capacity later as a moth primarily depends on the body mass accumulated during the larval stage. It is therefore of high importance to feed as much as possible in a short time span (Klemola et al. 2010).

In August – September the adult moths of the autumn moth fly to mate and then lay their eggs. However, the females of the winter moth cannot fly, which is why they have to walk to the top of the trees to mate and lay their eggs (Suomela et al. 1995). After all the eggs have been laid the moths die. Even though the winter- and autumn moth have similar biology, they differ in their ability to tolerate freezing temperatures and other abiotic factors (Huttunen et al. 2013).

3.4.3 Food preference

Autumn moth has the mountain birch as the main host but can compensate food shortage with understory species like dwarf birch, bilberry and northern bilberry (Karlsen et al. 2013). Studies on autumn moth have also shown that the larvae that complement their food of birch leaves with male catkins grew quicker and increased their body mass. It is of great survival importance if the larvae can eat a more nutritious food to pupate earlier to avoid predators (Klemola et al. 2010).

Since the winter moth originates from more maritime climates it is found throughout most of Europe. Its original main host is oak (*Quercus robur L.*) but do not show any discrimination in their selection of host plants in European forests (Wint 1983). It can also feed on hazel (*Corylus avellana L.*), blackthorn (*Prunus spinosa L.*) and different deciduous fruit trees (Feeny 1970). However, studies by both Feeny (1970) and Wint (1983) showed that during the maximum oak bud burst, this diet resulted in a greater reproductive success than alternative food sources. The winter moth, has since its population started to expand into the autumn moths' territory, also chosen the mountain birch as the main host. Thus there is not much knowledge in the preferred food species for winter moth in the arctic environments.

3.4.4 Predators

The predators and parasites that feed on the moths need to narrow their foraging to a short time peak corresponding to high moth abundance (Vindstad et al. 2011). The moths have many predators throughout their life cycle. As larvae they are attacked by insect-eating birds and spiders, moth pupae fall prey to shrews and predatory beetles and as adult moths they need to avoid bats, birds and harvestmen. Furthermore there are parasitic wasps that attack the eggs, larvae and pupae (Hansen et al. 2009). A changing climate with higher temperatures might change the outbreak patterns. Warm winters reduce egg mortality, resulting in a larger spring larvae population density, and lower spring and summer temperatures favours the moth with reduced parasitoid and predator activity (Young et al. 2014).

3.4.5 Competition

Since the winter moth has expanded into the autumn moths' territory, direct or indirect competition should be a likely event. That could explain why the winter moth has an outbreak cycle after the autumn moth (Ammunét et al. 2010). Studies on larvae performance between the autumn- and winter moth suggest however that neither direct nor indirect inter-specific competition between them reduced growth rate. Instead the winter moths' larvae actually had a higher survival rate when living together with autumn moths. Neither competitor are capable of suppressing the moth outbreak range and are unlikely causes for the time difference in the outbreak cycles (Ammunét et al. 2010).

4. Method

4.1 Study area

The study area was around Tromsø in northern Norway (69°38'56.6''N 18°57'17.1''E) that has an oceanic climate with mild and snow-rich winters and cool summers. The annual precipitation is ~ 1000 mm and the mean temperature in January is − 4.4°C and in July 9.1°C (Birchmoth 2015). The vegetation of the region is coastal mountain birch forests (*Betula pubescens* ssp. *czerepanovii*) with understory species like dwarf birch (*Betula nana*), bilberry (*Vaccinium myrtillus*), northern bilberry (*Vaccinium uliginosum*), black crowberry (*Empetrum hermaphroditum Hagerup*), lingonberry (*Vaccinium vitis-idaea*), bog-rosemary (*Andromeda polifolia*) and deciduous species like rowan (*Sorbus aucuparia*) and willow (*Salix caprea* & *Salix lapponum*).

The outbreak pattern is different from site to site around Tromsø because the terrain is very varied. The outbreaks are more local and not widespread over a larger area. The population of autumn moth started to rise around 2008 – 2010 and the winter moth followed approximately two years after. The autumn moth is now (2015) at the end of the outbreak and the population is about to collapse. It has already collapsed in some areas and the winter moth will soon reach its peak (Jepsen Personal communication).

4.2 Field method

4.2.1 The experimental set-up

The field experiment was performed in the early growing season, 2nd – 29th of June 2015. For winter moth, a total of 15 boxes with 20 larvae in each box were set up, five boxes for each plant species. For autumn moth there were a total of 18 boxes with 20 larvae in each, six boxes for each of the three different plant species (Figure 1). Due to inability to distinguish between the moth species in the beginning, many winter moth larvae were classified as autumn moth. The recent outbreak of autumn moth had resulted in a lower population in some areas. Extra boxes for autumn moth were therefore set-up to ensure equal amounts of larvae between the two moth species. The scarce umber moth was not included in the study due to its much lower population number. To find the right amount of larvae for the study would have been difficult.

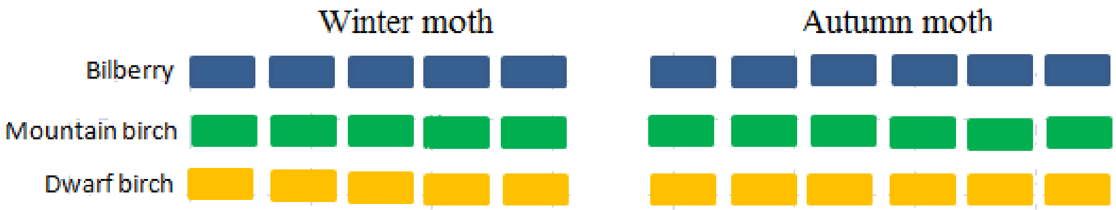

Figure 1: The set-up of the different food sources for the two moth larvae. The squares represent the different boxes and the colours indicate which plant species that was fed. The blue boxes always contained bilberry, while the green boxes contained mountain birch and the yellow boxes dwarf birch. The boxes also got an individual number to keep track on exactly which box that was handled.

All the boxes were first filled with moss on one side to maintain a good level of moisture. This also prevented the leaves from decaying quickly. For the start of the experiment, ~ 7g (fresh weight) of bilberry-, mountain birch- and dwarf birch leaves were put in five boxes each for winter moth and six boxes for autumn moth (Picture 8). The bilberry stems were always wrapped in wet paper and put in a plastic bag to last longer and the dwarf- and mountain birch were sprayed with some water before placed in the boxes. The boxes containing the larvae were kept in an illuminated room with a constant temperature of 15°C to ensure optimal growth of the larvae.

Picture 8: The three different boxes (Belsing 2015).

4.2.2 Field sampling

All samples for feeding material and larvae were collected within a 10 km distance around Tromsø. A total of 660 larvae were picked. The larvae were mostly in the second instar and still very small. Approximately five trees for mountain birch and eight shrubs for dwarf birch and bilberry, where two branches were cut from each tree and shrub, were chosen each time new food was required. All the larvae shared leaves from the same plant individuals, but the trees and bushes used to feed them were different for each feeding occasion.

4.2.3 General method

The leaves in the boxes were changed every fourth day to ensure that the larvae got fresh leaves to feed on. The old leaves were removed to prevent decay. The amount of leaves was increased further into the experiment as the larvae became bigger and ate more.

With the first changing of leaves the larvae that had been misclassified by species were put in the correct box to more easily keep track on the two species. The leaves used for refilling were also checked in order to eliminate the risk of putting new larvae into the boxes. Further, the old leaves had to be thoroughly checked when removed in order to make sure that all the larvae remained in the box. When changing the leaves, the number of larvae carcasses were noted and removed.

At the third changing of leaves, the larvae that were too small to have been inserted at the start of the experiment, or the incorrect species were thrown out. Half of the mosses were also removed and filtered sand was added to facilitate pupation. Over the whole study period, the boxes were refilled with leaves five times and at the 28th of June, the experiment was ended.

4.2.4 The larvae and pupae

At the end of the experiment, the pupae from each box were counted, dried at 60° for 48h and weighed separately. Each of the pupae got an individual ID depending on moth species, food species, box number and which order the pupae were weighed. This ID enabled comparison of the pupae weights between the two moth species and between the food sources. The larvae that had not yet pupated were counted to be able to calculate the total survival rate of the moth larvae depending on which food species they had been feeding on.

4.2.5 Frass and moisture content

The frass (Picture 9) were removed at every change before the new leaves were added and the larvae were put back into the boxes. The frass were swept up with a brush into a paper bag that got a different ID depending on which box it came from; box number, food species and moth species. The frass were then dried at 60° for 48h and then weighed to get the dry weight.

Picture 9: The frass is the brown cylindrical shapes next to the leaf (Belsing 2015).

Leaves from mountain birch, bilberry and dwarf birch were also always at every refilling accurately weighed (fresh weight) before being dried at 60°C for 48h and then weighed again (dry weight) to get the moisture content within the leaves. This was done to be able to assess the question about the leaves digestibility.

4.3 Statistical analysis

4.3.1 The statistical program and test selection

All the statistics were computed in IBM SPSS Statistics 23 Armonk, New York. The data for the individual pupae- and frass weights (g) were first tested for normality with the Kolmogorov-Smirnov and Shapiro-Wilk test ($P > 0.1$). If the data was normally distributed an ANOVA test with a post-hoc Tukey test for multiple comparisons could be chosen ($P < 0.05$). If the data was not normally distributed, the non-parametric test Kruskal-Wallis was chosen. The Kruskal-Wallis test ranks the data and presents a mean rank value and a Chi-square significance value. The Chi-square test tells if there is a relationship between two categorical variables ($P < 0.05$). A Pearson correlation test was also used to see if there is a linear relationship between two datasets. For all the statistical analyses, if the P-value is less than 0.05 there is significance, and if less than 0.001 there is a strong significance.

4.3.2 Food preference and digestibility

The Shapiro-Wilk test proved that the data for pupae weight was normally distributed. An ANOVA test was therefore chosen. It was run to see if the pupae weights (g) differed between the two moth species and if the plant species given affected the pupae weight for either moth species.

In order to assess if there was any difference in the frass weight (g) between the moth species and the food species a Kruskal-Wallis test was chosen. This test was chosen since the frass weight was not normally distributed.

As an index to leaf toughness with lower moisture content, the moisture content was also calculated for the leaves according to:

$$M_C = \frac{(W_F - W_D)}{W_F} \times 100$$

M_C = Moisture content (%)
W_F = Fresh weight (g)
W_D = Dry weight (g)

Since the moisture content data was normally distributed, an ANOVA test with a post-hoc Tukey test could be performed against plant species.

4.3.3 Survival

Survival rate (%) was calculated for only pupae (pupae survival rate) and living larvae and pupae together (total survival rate). First the number of larvae that went into each box was recalculated since some larvae in the beginning had been classified incorrectly. A Kruskal-Wallis test with multiple comparisons was chosen for both the moth species to see if the total survival rate and food species were linked. These datasets were not normally distributed. A Pearson correlation was also performed between the average pupae weight in each box and the survival rate for pupae to see if larvae that had gained a bigger pupae weight had a higher survival rate.

5. Results

5.1 Comparison between the two moth species

According to the statistical analysis there was a strong significant difference between the two moth species pupae weight (g) (df1 = 1, df2 = 218, F = 75.234, $P \leq 0.001$), where the autumn moth was larger than the winter moth (Figure 2).

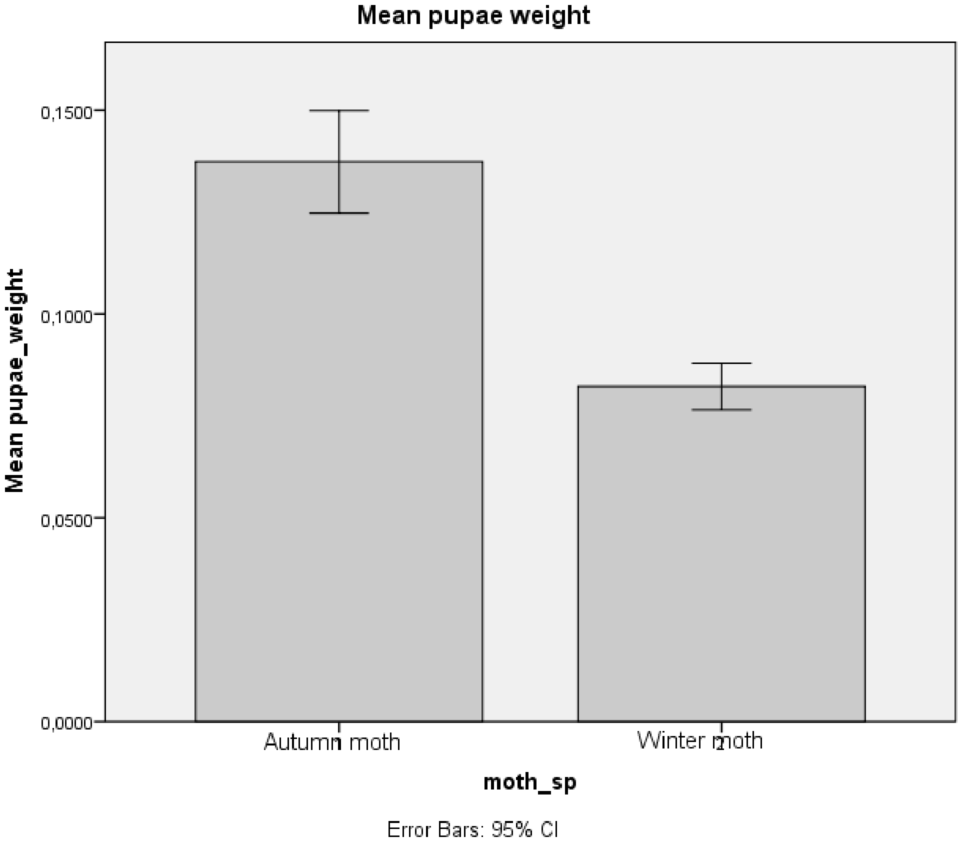

Figure 2: The pupae weight (g) for autumn moth was significantly larger than winter moth.

The frass weight (g) did not differ significantly between the two moth species (df = 1, $Chi^2 = 1.418$, P = 0.234), with a mean rank frass weight score of 82.16 for autumn moth and 73.15 for winter moth.

There was no difference in the total survival rate (%) between the two moth species (df = 1, $Chi^2 = 0.158$, P = 0.691).

The total number of pupae which developed from both moth species was not correlated to the gained weight (r = − 0.096, N = 33, P = 0.597). The total number of pupae that was developed for both moth species is illustrated in Table 1.

Table 1: Total number of larvae that developed into pupae for the different food treatments and the average pupae weights for each food source.

	Autumn moth		Winter moth	
	Nr. of pupae	**Avg. pupae weight (g)**	**Nr. of pupae**	**Avg. pupae weight (g)**
Bilberry	25	0,144	42	0,075
Mountain birch	16	0,119	21	0,071
Dwarf birch	50	0,143	65	0,090
Total	*91*	*0,406*	*128*	*0,237*

5.2 Autumn moth: comparison between food sources

When comparing if the food species influenced the moth species pupae weight (g), it proved not to for the autumn moth (df1 = 2, df2 = 89, F = 1.799, P = 0.172) (Figure 3).

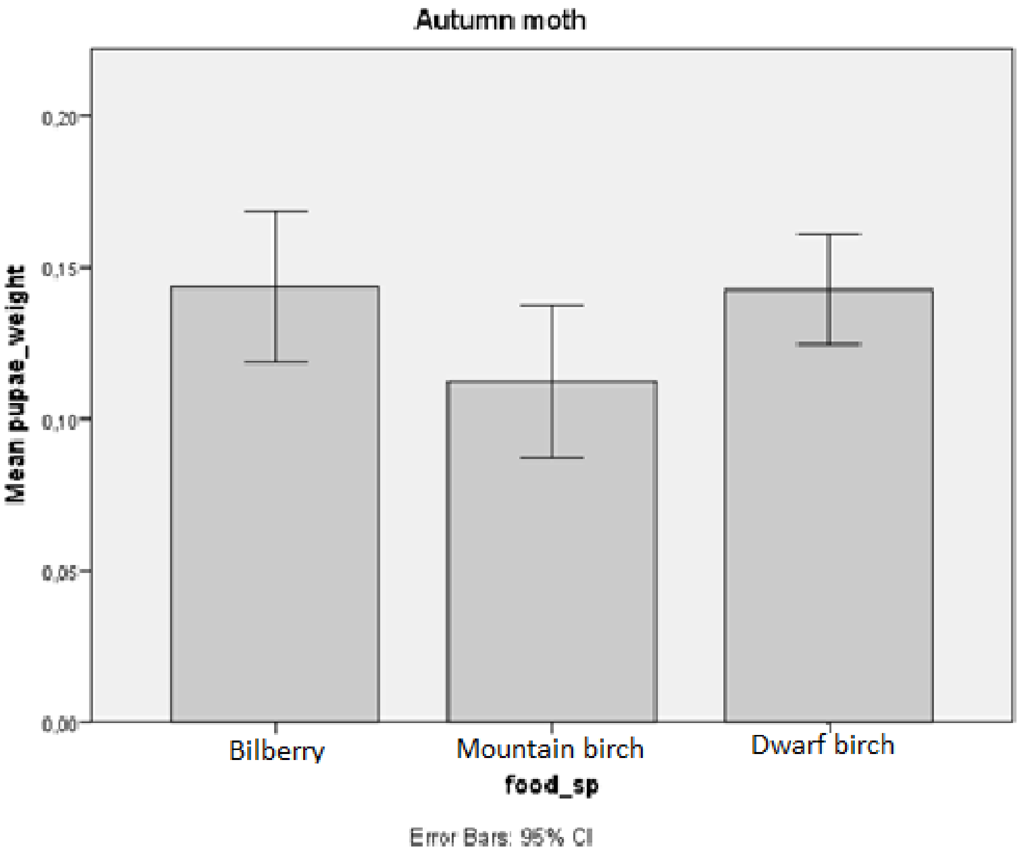

Figure 3: There was no significant difference in the pupae weight (g) between food sources.

The frass weight (g) also proved to not statistically differ between the food species for autumn moth (df = 2, Chi^2 = 2.118, P = 0.347) (Figure 4).

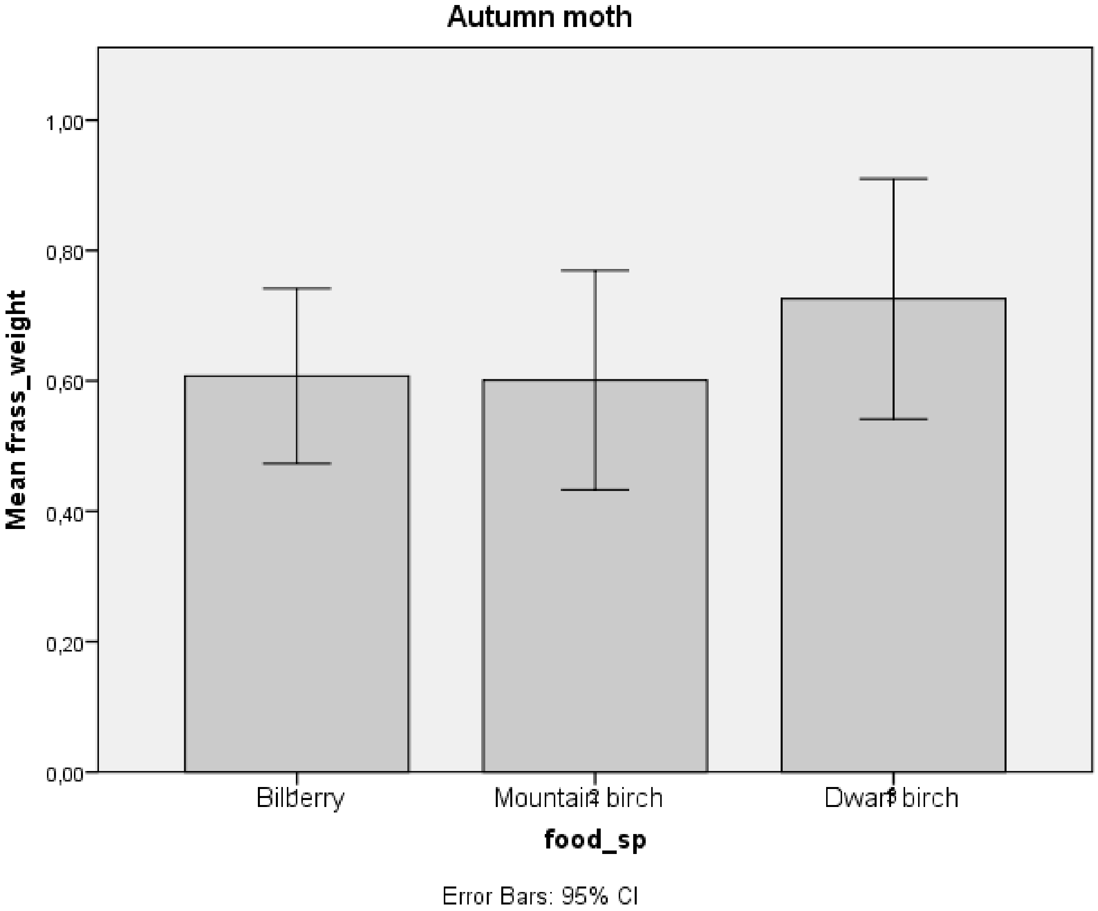

Figure 4: There was no statistical difference in frass weight (g) between the food sources.

There was no correlation between the pupae survival rate (%) and pupae weight for autumn moth (r = 0.377, N = 18, P = 0.123).

For autumn moth there was an overall significant difference in the total survival rate among food species (df = 2, $Chi^2 = 10.408$, P = 0.005). Specifically, the larvae feeding on dwarf birch survived better when compared to the larvae that ate bilberry (P = 0.009) and mountain birch (P = 0.004). There was no difference in the survival rate of larvae between bilberry and mountain birch (P = 0.240) (Figure 5).

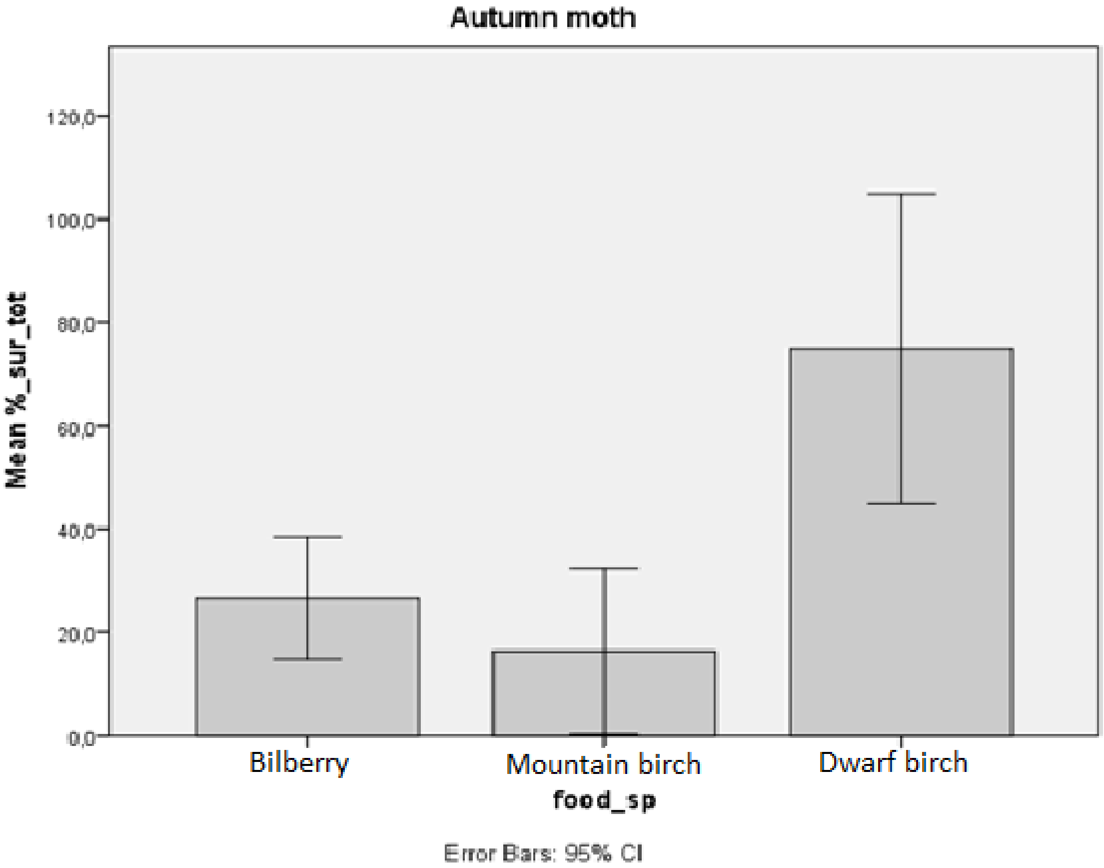

Figure 5: Feeding on dwarf birch resulted in highest survival rate (%) for autumn moth.

5.3 Winter moth: comparison between food sources

There was an overall statistically significant difference for winter moth when comparing if the food species influenced the pupae weight (g) (df1 = 2, df2 = 125, F = 4.331, P = 0.015). Specifically, the pupae weight for winter moth when feeding on dwarf birch was larger when compared to mountain birch (P = 0.050) and bilberry (P = 0.048). There was no difference in pupae weight for winter moth between bilberry and mountain birch (P = 0.892) (Figure 6).

Figure 6: There was a significant difference in pupae weight (g) between the food sources.

The frass weight (g) proved not to statistically differ between the food species for winter moth (df = 2, Chi^2 = 0.638, P = 0.727) (Figure 7).

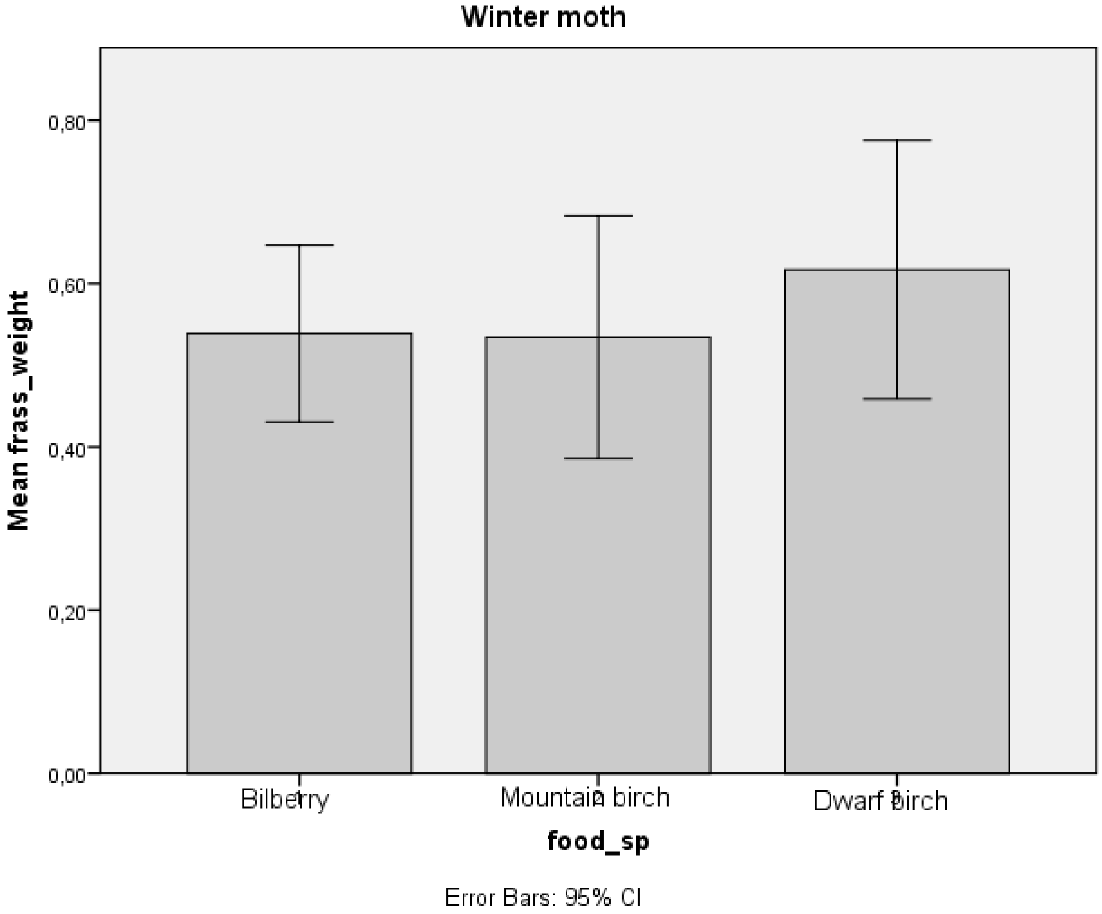

Figure 7: There was no significant difference in frass weight (g) between food sources.

There was no correlation between the pupae survival rate and pupae weight for winter moth (r = 0.245, N = 15, P = 0.378).

For winter moth there was no significant difference in the total survival rate (%) between food species (df = 2, $Chi^2 = 4.531$, P = 0.104) (Figure 8).

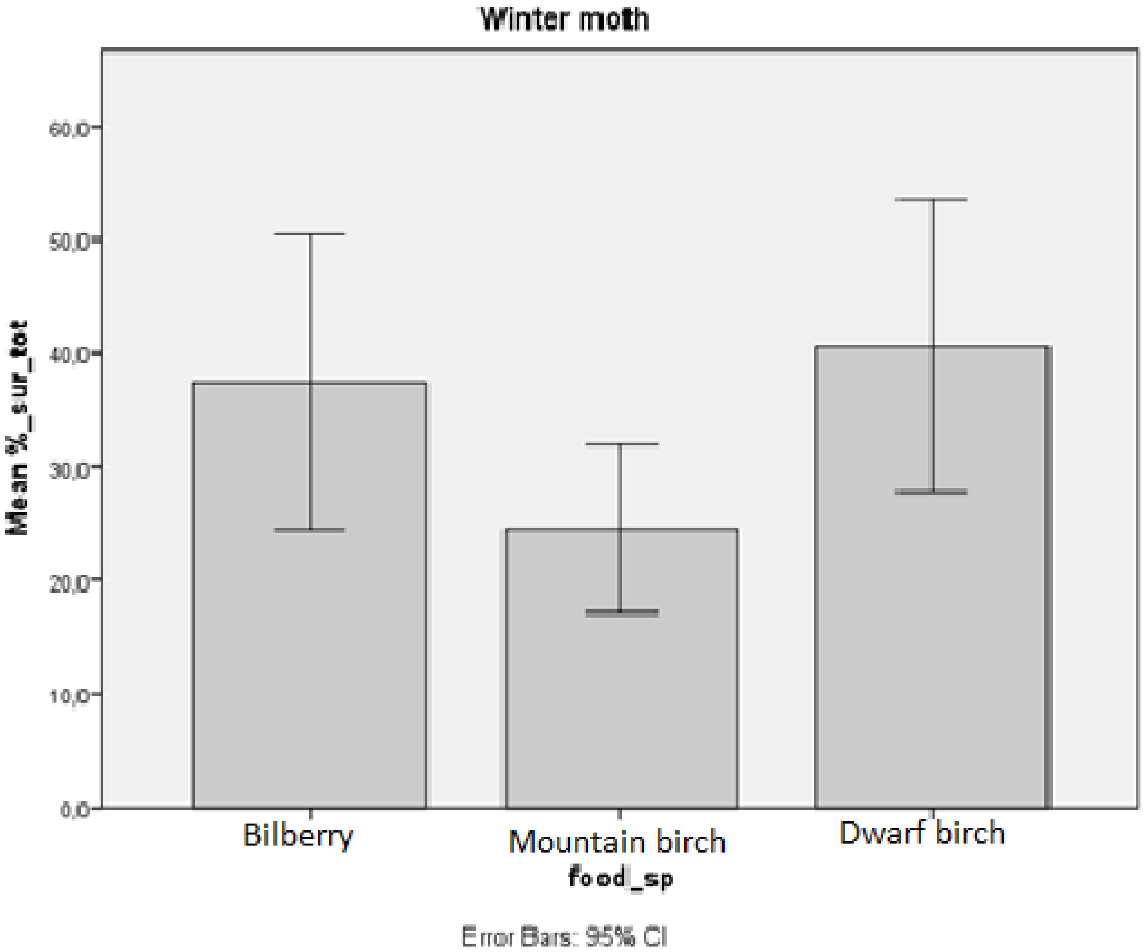

Figure 8: There was no significant difference in survival rate (%) between the food sources.

5.4 Moisture content: comparison between food sources

The moisture content (%) of the leaves that were given to the larvae were significantly different (df1 = 2, df2 = 15, F = 10.317, P = 0.002). The leaves of dwarf birch contained less water than mountain birch (P = 0.002) and bilberry (P = 0.007), but there was no difference between mountain birch and bilberry (P = 0.809) (Figure 9).

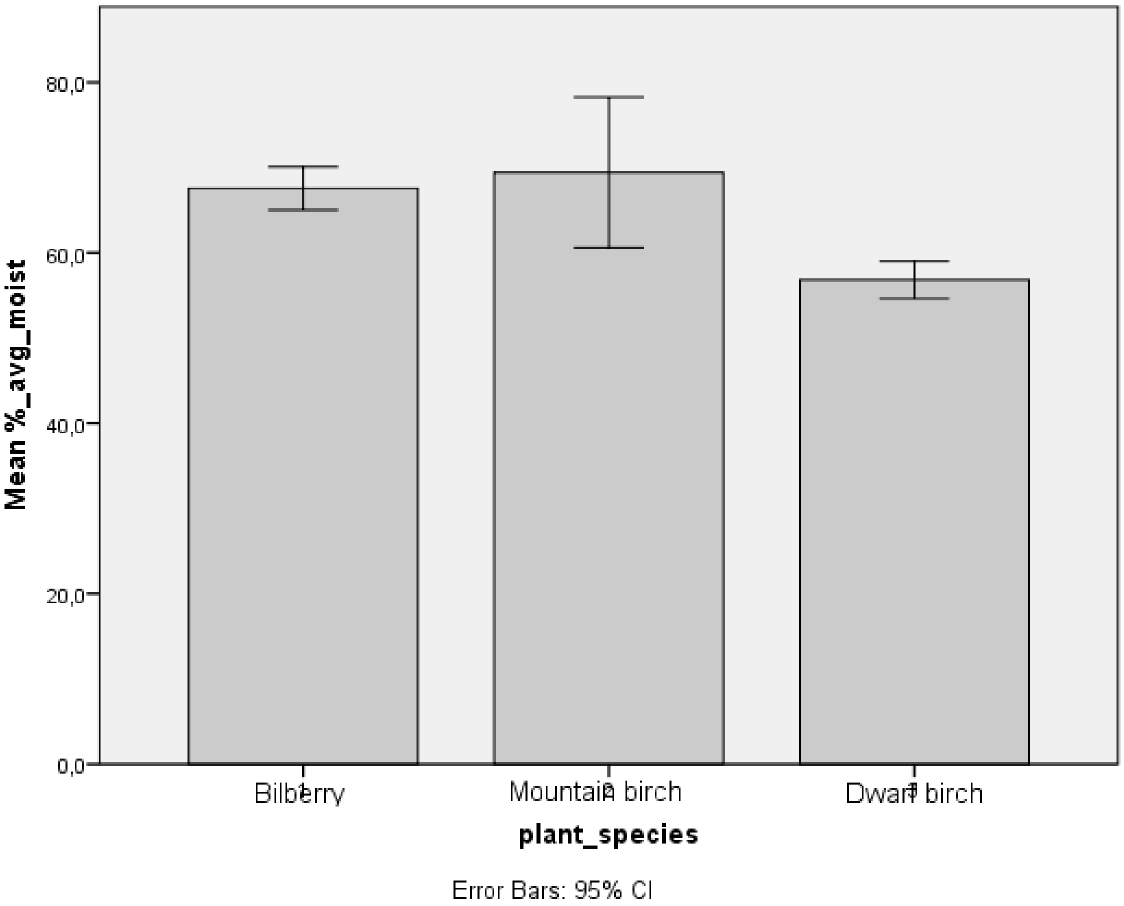

Figure 9: The average moisture content (%) of the leaves that were put into the boxes for feeding, where dwarf birch contained the least.

6. Discussion

6.1 Question 1. Food preference

The first question asked was if the larvae would develop smaller pupae if feeding only on non-preferred understory species? The growth was quantified by measuring pupae weight after a fixed time period. This study found little pattern in pupae weight, only a weak pattern opposite to that expected, with greater pupae weight developed from understory species. Specifically, when first comparing the difference in gained pupae weight between the two moth species (Figure 2), the pupae weight between them differed, which was expected since the larvae of autumn moth are larger in the field. Autumn moth showed no significant difference in the pupae weight between the food sources (Figure 3). The pupae weight for winter moth (Figure 6), however, was significantly larger after feeding on dwarf birch leaves than bilberry- and mountain birch leaves. No studies on winter moths' performance in the arctic environments aside from this study could be found, so these findings provide valuable new data about this important species.

The findings of this study about food preference are surprising because according to Hanhimäki et al. (1994), who studied autumn moth in northern Finland, the dwarf birch is supposed to be a poorer food source for the moth larvae than mountain birch. Yang et al. (2008) studied the development time to pupae and difference in pupae weight for autumn moth in northern Finland. They also found that mountain birch leaves were the best food for the larvae compared to dwarf birch (Figure 10). However, when looking at the result from Figure 3 and 6 the results from this study do not follow that trend. In Figure 10, the pupae weight for autumn moth for dwarf birch and northern bilberry is very similar. This was also the case for autumn moth in this study, but not for winter moth where dwarf birch got significantly larger than the other two food species. The study by Yang et al. (2008) also included northern bilberry and not bilberry. In this study, on the third refill northern bilberry mixed with bilberry was also accidentally added to the bilberry boxes. However, it might be possible to assume that northern bilberry and bilberry would give comparable results due to their very similar phenology. Bilberry and northern bilberry belong to the same genus, can grow on similar places and flower at the same time (Olsson and Nylén 1985).

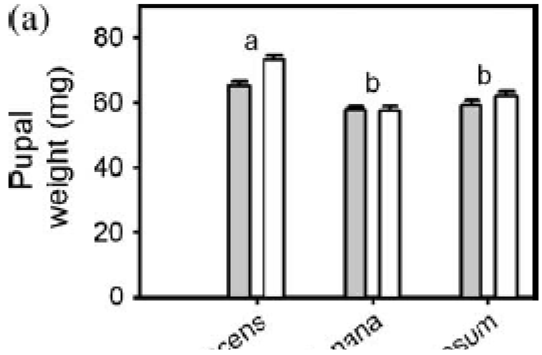

Figure 10: Difference in pupae weight for autumn moth between plant species and males/females (Yang et al. 2008).

6.2 Question 2. Digestibility

The question here was if one food source would result in more frass. This study found no clear evidence to confirm this since the frass amount did not differ for the two moth species, or between the food sources (Figure 4 and 7). However, the Kruskal-Wallis test is not as strong as an ANOVA, so there might have been a difference if a more powerful test could have been performed.

The leaves of dwarf birch are considered harder to digest (Ruuhola et al. 2013) but did not result in more or less frass. The lack of differences suggests that no matter which of the three different plant species the moth larvae feed on, none is producing more frass that could promote graminoid expansion (Jepsen et al. 2013). But according to Jepsen et al. (2013), large outbreaks in nutrient poor locations in northern Norway changed the vegetation type towards graminoid dominance, which indicates that the input from herbivores must be of importance. If more nutrients would be added to the ground due to more nutrient-rich frass, this will have a great impact. However, without a nutrient analysis it is impossible to tell if one of the food sources resulted in more nutrient rich frass.

A vegetation shift due to added nutrients would change the resource availability and this can affect the ecosystem biochemistry and climate sensitivity. The arctic environments have a low soil temperature and high moisture content through much of the growing season, which result in low nutrient cycling between plants and soil (Nadelhoffer et al. 1997). Increased temperatures enhance the availability of nutrients and nitrogen addition increase growth in many species. Due to this, it is predicted that there will be a 30 – 50% loss of species with higher temperature and more nutrients, conditions that favour some species over others (Chapin et al. 1995).

Figure 11 illustrates the hypothesized effects of insect herbivory on the ecosystem nutrient cycle. It indicates that the added nutrients to the soil are greater with the herbivores involvement. As written above, the herbivores might provide a shortcut for the nutrients to reach the soil (Kaukonen et al. 2012). The herbivores can thereby alter the amount and types of organic matter that reach the soil. So the effects on the nutrient cycle with increased temperatures might be greater with herbivory than without. That is why it is of a high importance to fully investigate the influence of insect herbivores on the nutrient cycle.

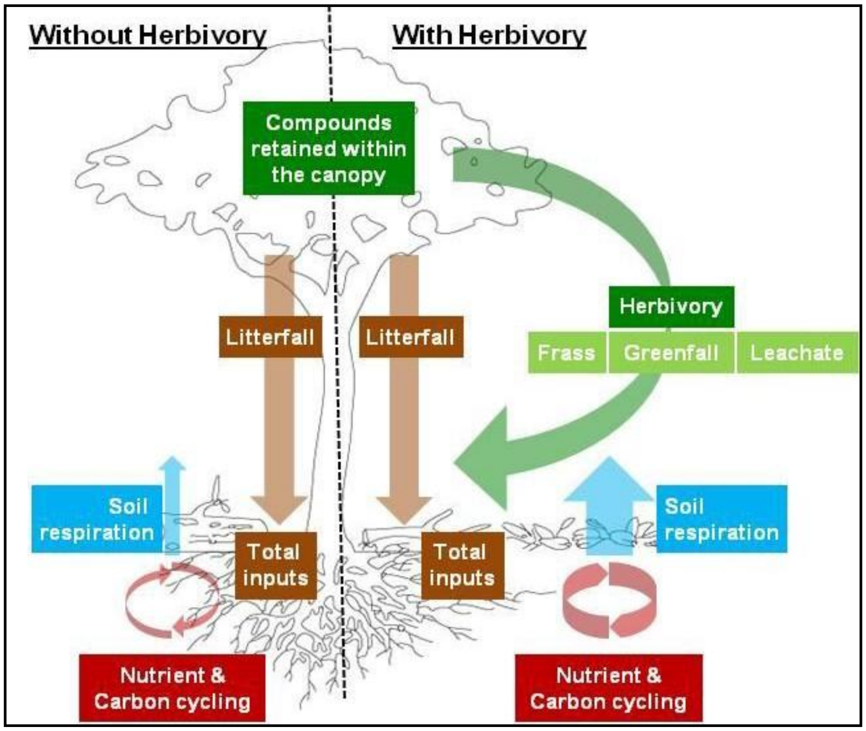

Figure 11: Illustrates possible effects of herbivory on ecosystem nutrient cycle. Herbivores constitutes an important additional pathway for nutrients to the soil via frass, greenfall (unconsumed leaf fragments) and leachate, where it potentially alters a range of soil processes (Metcalfe 2015).

6.3 Question 3. Survival

This study question asked which food source will result in the most optimal growth and survival of the moth larvae? The results found little clear consistent effect of food source on either growth or survival. To begin with, there was no difference in the total survival rate between the two moth species. The total number of pupae was not correlated to the weight either, suggesting there was no competition between the larvae in the boxes. For both moth species there were no correlation between the pupae survival rate and the average pupae weight. The larvae that had gained a higher pupae weight did not have a higher survival rate, which implies that greater mass does not always lead to better survival. This might be due to the fact that the pupae of autumn moth were bigger but the total number of pupae was greater for winter moth, as seen in Table 1.

Even though the pupae weight for autumn moth did not differ between the food sources, the survival rate did (Figure 5). Those who were fed on dwarf birch survived better than when feeding on bilberry and mountain birch. For winter moth it was the opposite, with a difference in pupae weight but no significant difference in survival among food groups (Figure 8). Since there was no difference in survival rate this implies that winter moth adapted more easily to the different food species. A reason for this can be because the winter moth comes from more southern regions which may explain its ability to have more than one plant species as a host. This agrees with the study by Wint (1983) who examined winter moth’s growth and survival on their primary host oak (*Quercus Robur L.*), and five common alternative plant species; hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa L.*), hazel (*Corylus avellana L.*) beech (*Fagus sylvatica L.*) and cultivated apple (*Malus sylvestris Mill.*). The study revealed that even though the winter moth seemingly preferred to feed on oak, the larvae had no problem growing sufficiently feeding on the alternative plant species in the absence of oak. Wint et al. (1983) also concluded that the winter moth larval polyphagy is an adaptation to counteract the effects of using an unpredictable primary food source. Furthermore, the larvae have a low resistance to starvation and have to disperse in search for food if its initial food source should be unsuitable.

For winter moth, the total survival rate also followed how the pupae weights were distributed between the food sources. The food species that gave the best survival rate also resulted in greatest pupae weight. By contrast, for autumn moth there was quite a difference in pupae weight and survival differences among food sources. For example, the pupae weight for autumn moth when feeding on bilberry was quite large but the total survival rate was low.

Since mountain birch is the main food source for autumn- and winter moth, it was unexpected in this study that the moth larvae fed on mountain birch achieved a similar or sometimes lower pupae weight and survival rate compared to larvae fed on alternative food species. The total amount of dead larvae throughout the experiment was highest on mountain birch for both species. There might therefore have been an unknown factor that caused the death of the larvae. The researcher on Birchmoth, Ole Petter Laksforsmo Vindstad, confirmed that the larvae sometimes suffered from virus infections. However, it should have been likely that the infection would have spread between all the boxes in the experiment. Even if there is no shortage of food and they lived during optimal temperature, it might therefore have been inter-specific competition for space. However, Ammunét et al. (2010) could not find in their studies of larvae performance any causes for competition.

An explanation could be that the recent outbreaks have forced the mountain birch to produce less nutritious leaves. The birch forest might have become weakened in some areas and unable to sustain then high nutrient demands from the larvae. The leaves that sprout from defoliated trees also contain less water, which make them harder to digest (Huttunen et al. 2013). However, according to the moisture content (Figure 9), the mountain birch leaves still contain the highest moisture content. Thus, there are no clear reasons to doubt the study finding that the key food group for the moths, the mountain birch, appears to inhibit moth survival. Further work in this area is required to advance the understanding of the underlying factors driving these interactions.

6.4 Leaf properties

Since dwarf birch contains less moisture (Figure 9) it would likely have higher leaf toughness (Huttunen et al. 2013). The dwarf birch also contains more tannin than the other two plant species (Ruuhola et al. 2013), which should make the leaves distasteful and hard to digest. This seems not to be the case for this experiment. When collecting the leaves for the experiment, larvae were often found on mountain birch- and bilberry leaves, especially further into June when the weather started to stabilize. Larvae were seldom found on dwarf birch leaves and it does not seem like their population suffered from outbreaks. The bilberry plants however, seemed to have suffered badly from the earlier years of the outbreaks. There were hardly any plants with leaves on. Many butterfly larvae were also found on the bilberry plants, but not on the other two species, which indicates that bilberry is a favourable food choice for other herbivore species. It might not only be the moth larvae that caused the severe defoliation.

Bilberry plants do not use chemical traits to defend themselves against herbivores to the same extent as the other species (Laine and Henttonen 1987), and that could be one answer to why the plants have suffered badly from the ongoing outbreaks. The question is then why there are not more moth larvae feeding on the dwarf birch in the studied area? An explanation could be that the females of winter moth cannot fly when ovipositioning, and have to lay their eggs on the trees or underground where they have become an adult moth. The autumn moths on the other hand can fly, though not for very long distances. Bilberry is a major component of the understory species community in the area where the moths live and is therefore easy to access. The dwarf birch on the other hand, either grows above the tree line where the leaves sprout later than the below vegetation, or on swampy areas, which might be harder for the moths to access. Therefore, maybe it is not that the larvae have a problem to digest the leaves but a problem to reach the dwarf birch in a sufficient amount to cause widespread defoliation as for the mountain birch forests and bilberry populations.

Another explanation could be that the depth and duration of snow cover is important in terms of the functioning of arctic ecosystems. The snow protects plants and soils and provides moisture to the soil in the beginning of the growing season (Torp et al. 2010). In arctic regions, both temperature and precipitation are predicted to increase and snow cover is expected to decrease in most areas. However, snow depth might increase in arctic regions where a large amount of elevated precipitation will fall as snow. The duration of snow cover will be dependent on whether warmer spring temperatures can compensate for increased winter snow depth (Torp et al. 2010). Tromsø already experiences snow-rich winters, but there is also a weak trend towards increasing snow depth measured since 1945 (Vikhamar-Sculer et al. 2010). With increased temperatures, the plant functions will also be modified. Altered snow conditions can influence the interactions between plants and their herbivores and the snow cover can change the plants phenology. A prolonged snow cover might increase the plants nitrogen concentration and increase the mineral nutrient availability (Torp et al. 2010). As such, the food source for the herbivores may get more nutritious. A study by Torp et al. (2010) on autumn moth in Abisko, northern Sweden, proved that the moth larvae grew faster when feeding on dwarf birch that had more snow cover during winter. The increase of nitrogen might also override the effects of chemical substances in the leaves, like tannins (Torp et al. 2010).

Since the sub-arctic is predicted to experience an increased drought pressure (ACIA 2004), it is difficult to say which change will have the greatest effect on specific areas. The initial state of the forest will also create different scenarios. And as the study by Graglia et al. (2001) confirmed, the tannin production varies a lot between the dwarf birch populations. Therefore it might not be the case for the Tromsø region that the dwarf birch is hard to digest.

6.5 Ecosystem effects

A key impact of moth activity in arctic ecosystems will be in regulating available nitrogen under future climate shifts. Nitrogen limitation affects the plants growth more than the cold conditions. Addition of nitrogen to already thawing arctic environments has also greater effects on ecosystem net carbon gain than increase of atmospheric carbon dioxide (Nadelhoffer et al. 1997). If the arctic ecosystem is very nutrient limited warmer temperature alone will not increase the plant production (Chapin et al. 1995). Nitrogen addition can stimulate decomposition of stored SOM (soil organic matter) with possible consequences on the global climate (Wild et al. 2014). It will also cause a higher absorption of other ions and this will alter the carbon balance (Chapin et al. 1995). These combinations might permit greater impacts of climate change. It will be difficult to predict the future changes since species response to climatic changes are very individual and not easily generalised (Chapin et al. 1995). This study makes a first contribution towards understanding some of these moth- and plant species-specific interactions.

The moth larvae are dependent on the weather. If it is cold and wet they will not develop, but as soon as it gets warmer they grow very quickly (Jepsen Personal communication). Since this June (2015) was very cold and wet the larvae stayed in their third instar for many weeks and the growth rate was very slow. However, cold weather does not kill the larvae it only prolongs their development time. The sub-arctic is already experiencing the increased threat of infestation of moths (Amundsen and Lie 2014). If the mountain birch forests are affected negatively by a warmer climate, the moths will probably still threaten the vegetation, since they seem to be not fully dependent on mountain birch according to the results of this study and are therefore not strongly limited by its abundance.

The effects of climate change are likely to be most pronounced in the Arctic (ACIA 2004), but for the moths the altitudinal climate changes can be more severe than the latitudinal changes e.g. altered wind patterns (Bale et al. 2002). The survival of the moths can also vary between the moth species, which plant species they are feeding on and has as a main host (Bale et al. 2002). The variations that lies within both the moth- and plant populations, and depending on which area they come from, might have a greater impact than previously thought of.

Also, herbivorous species that occupy different habitat types across a range of latitudes, e.g. winter moth, show a high phenotypic and genotypic plasticity (ability to change the physiological appearance and development in response to changes in the environment) (Bale et al. 2002). The ability to deal with a range of host plants, including low quality ones, may indicate their ability to cope with climate change. Compensatory feeding may be the key to survival. They are less likely to be negatively affected by climate change, as other species that occupy narrow niches (Bale et al. 2002). The distribution range of the moth species is not well understood but is most likely due to a combination of factors. Climatic conditions, natural enemies, host phenology, competition, forest age structure and resource distribution are all likely to play an important role (Jepsen et al. 2008).

The autumn- and winter moth have a similar biology but differ in their ability to tolerate freezing temperatures (Huttunen et al. 2013). As Wint (1983) concluded in their study, and was the result in this, the winter moth is not limited by only one plant species as a host. It has the ability of compensatory feeding. From the results in this study it seems that the autumn moth is also capable of some compensatory feeding. However, the survival rate differed for autumn moth more than for winter moth and its populations do not occupy that many different habitat types. With increased temperatures in the arctic environment it is likely that this will favour the winter moth population and other invasive moth species like the scarce umber moth. Even though there is no direct competition between the two moth species now, that might change in the future. The winter moth has also over the past years expanded more and more into the autumn moths' domain, but the autumn moth has also started to occur even in the coldest most continental regions (Jepsen et al. 2008). There might therefore be possible in the future that the winter moth will take over many of the autumn moths domain, while the autumn moth is moving into territories that were too cold before but is now inhabitable. The moth species ability to easily change the main host when one is unavailable, e.g. damaged from outbreaks, can cause a more direct threat to the arctic vegetation. When new species are introduced in an ecosystem is a key question as well, which remains largely unknown, will the local predators be able to control this new inhabitant and restrict the outbreaks?

6.6 Improvements and future work

Improvements of this study could be to rear the moths already in their egg form to be certain to get equal amounts of individuals from both moth species. To keep the larvae in more natural conditions, outdoor, and include more plant species and have a greater sample size. To avoid any chance of competition in the boxes, the larvae could have been reared individually in small plastic jars. Then it would have been easier to see if larvae were added with the food and remove them quicker. Also have a longer study period where all the larvae would have gotten a chance to pupate, and then see how many of the pupae that actually survived.

Further studies could have examined temperature effects on moth survival and feeding rates since these environments are climate sensitive. Studies that also included the pathway of nutrients, generated from leaf consumption by the moth larvae, might as well help to address some uncertainties in this study. A question for the future is furthermore how the predation pattern will change with higher moth populations and climate change.

7. Conclusion

Since outbreaks by moth larvae are one of the most important natural disturbance factors in the mountain birch forests, it is of importance to see how the larvae will cope to alternative food sources. Depending on how they cope, they may have a different impact on the ecosystem functioning in the future. For this study the pupae weight did not become smaller when feeding on understory species, which were not the preferred food species. Instead, feeding on the preferred species mountain birch generated the lowest pupae weight and survival rate. The amount of frass generated did not differ between the two moth species or between the food sources. The lack of differences suggests that no matter which of the three different plant species the moth larvae feed on, none is producing more frass that could promote graminoid expansion. If more nutrients would be added to the ground due to more nutrient-rich frass, this will though have a great impact.

For autumn moth there was no significant difference in the pupae weight between the food sources, but there was a better survival rate when feeding on dwarf birch. For winter moth it was the opposite, with a difference in pupae weight among food sources but none for survival rate. Since there was no significant difference in the total survival rate for winter moth, it seems like this moth species adapted more easily to the different food sources. A reason for this can be because the winter moth comes from more southern regions, which may explain its ability to have more than one plant species as a host.

With a changing climate and more severe outbreaks on the mountain birch forests, the forests might suffer very badly and might not recover in all areas. A different food pattern of the moths with other plant species as hosts might change the nutrient cycle and permit greater impacts of warming than would otherwise occur. A greater infestation of moths in these sensitive ecosystems can also alter the already ongoing climate changes and cause vegetation shifts that would result in a loss of many important key species. Further studies that include temperature differences and the pathway of nutrients are needed to address remaining uncertainties.

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Front picture: Belsing, U. 2015. *5th instar of winter- and autumn moth.* Taken 18/06 2015, in Tromsø.

Picture 1: Belsing, U. 2015. *Mountain birch forest.* Taken 03/06 2015, in Tromsø.

Picture 2: Belsing, U. 2015. *Mountain birch leaves (above) & male catkin (below).* Taken 07/06 2015, in Tromsø.

Picture 3: Belsing, U. 2015. *Dwarf birch leaves (above) & male catkin (below).* Taken 09/06 2015, in Tromsø.

Picture 4: Belsing, U. 2015. *Bilberry leaves and flowers.* Taken 10/06 2015, in Tromsø.

Picture 5: Belsing, U. 2015. *3rd instar of autumn moth.* Taken 07/06 2015, in Tromsø.

Picture 6: Belsing, U. 2015. *3rd instar of winter moth.* Taken 07/06 2015, in Tromsø.

Picture 7: Belsing, U. 2015. *3rd instar of scarce umber moth.* Taken 09/06 2015, in Tromsø.

Picture 8: Belsing, U. 2015. *The three different boxes.* Taken 08/06 2015, in Tromsø.

Picture 9: Belsing, U. 2015. *The frass is the brown cylindrical shapes next to the leaf.* Taken 08-06 2015, in Tromsø.

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