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Indirect effects of rodents on arthropods in a Scandinavian boreal forest

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Abstract

Rodents in boreal forest are an important component of food webs. Their role as drivers of the boreal forest ecosystem is debated. As herbivores they affect plant communities and alter qualities of plants. Consequently availability of food resources for other herbivorous species is altered. In my thesis I studied whether rodents indirectly influence communities of arthropods via plant resources. It is assumed that phytophagous arthropods respond to changes in plant resources by different feeding behaviour that further affects higher trophic levels including predators and parasites. I swept the arthropods in 96 plots at six localities in a boreal forest in Eastern Norway with different rodent densities in the months of June and August in 2014. I assessed abundance of arthropod orders and biomass of arthropod feeding guilds in relation to observed rodent populations. I found rodents were important for arthropod communities in the month of June, but not in August. All feeding guilds and orders Diptera and Collembola were correlated negatively, while orders Hemiptera, Thysanoptera and Opiliones were correlated positively with rodent density. I assume the relations I found are not necessarily the result of indirect interactions only, but potentially also of direct predation of rodents on arthropods, or the combination of both direct and indirect interactions. The influence of rodents seems to depend on vegetation type creating differently functioning systems. In addition, I briefly discuss the effects of environmental and habitat factors which were used to explain variance in the arthropods living in different conditions.

Contents

1. Introduction

Natural systems are highly complex, formed by abiotic environments and interacting organisms, that determine ecosystem processes and functioning (Holt & Loreau 2001; Janssen & Sabelis 2004). Recent scientific work in this field sets a clear direction for further research on ecological communities and demands extension of the focus from bilateral and direct interactions to multispecies and indirect interactions (Yodzis 1988; Ritchie & Olff 1999; Strauss & Irwin 2004; McGill *et al.* 2006; Ohgushi 2008). Several studies provide evidence on equivalent importance of indirect and direct interactions, whether it concerns the occurrence within a community (Menge 1995; Ohgushi 2008), intensity (Strauss 1991b; Miller & Travis 1996), or evolutionary formation of the interactions between species (Miller & Travis 1996).

An indirect interaction is defined broadly as a relationship between two organisms which do not interact directly, but which interact through mutual relationship with a third species or through habitat (Wootton 1994; Miller & Travis 1996). By definition, it is an attribute of multispecies environments (Strauss 1991b). Over several decades, an adequate classification system of indirect interactions has been discussed (Miller & Kerfoot 1987; Strauss 1991b; Wootton 1993; Billick & Case 1994; Wootton 1994; Wootton 2002). Nowadays, it seems ecologists have adhered best to Abrams's classification (see eg. Werner & Peacor 2003; Wojdak & Luttbeg 2005), who distinguishes among density-mediated (DMII) and trait-mediated (TMII) indirect interactions (Abrams *et al.* 1996). DMII are transmitted through changes in population densities, whereas TMII through changes in traits - behavioural, morphological, physiological, and others. Abrams *et al.* (1996) referred to indirect interactions on the interface between DMII and TMII as mixed interactions.

This study focuses on indirect effects posed by rodents on phylum Arthropoda in the boreal zone. Rodents, hares and cervids represent three major groups of herbivorous mammals in boreal forests (Tahvanainen, Niemela & Henttonen 1991). They are known to be very important within food webs, as primary consumers and as prey for predators (Hörnfeldt *et al.* 1990). Their cyclic persistence has essential impact on the dynamic of Fennoscandian boreal forests. Rodents forage on plants that are sessile resources which are usually exploited by several consumers with non-lethal effects on the plant. This constitutes a good foundation for generating a multitude of interaction linkages (Ohgushi 2005). Indirect effects arising from interactions with the vegetation represent a major series within TMII and they are called plant-mediated indirect interactions (Ohgushi, Craig & Price 2007, p. 5). As

approximately half of all extant species of Hexapoda (Insecta), the largest class within phylum Arthropoda, is phytophagous, feeding solely on living plant tissues, effects of rodent grazing on vegetation are likely to affect communities of arthropods (Strong, Lawton & Southwood 1984). For herbivorous arthropods and their natural enemies, plants play a fundamental role by providing vital resources such as food, refuge and shelter. Features of plants and plant communities determine load of arthropods, carrying capacity for herbivorous species and interactions with predators and parasitoids (Schult 1992).

Although the indirect impact of rodents on arthropods can have many pathways, this study considers primarily plant-mediated interactions. Other possible indirect effects, e.g., through changes in ecosystem processes, are not within scope of the study.

Plants have developed various strategies as a response to herbivory. Depending on the strategy, they can affect herbivores through both - positive and negative feedbacks. Kaplan and Denno (2007) argued that already slight herbivory activates production of secondary metabolites, called induced responses, with either a defensive role – mitigating negative consequences of injury, or a resistant role – preventing further attack of herbivores (Karban & Myers 1989). These metabolites, also known as allelochemicals or secondary compounds, are aimed to reduce herbivory (Harborne 1991). They may accumulate rapidly (Green & Ryan 1972) or occur with delay the following season after damage (Tuomi, Niemelä & Siren 1990). However, responses among herbivores to secondary compounds are diverse. Several studies indicate that induction and effect of secondary compounds on herbivores differ from one species to another. These effects may be plant-specific (Geervliet *et al.* 1997), as well as herbivore-specific (Karban & Baldwin 1997, p.20; Agrawal 2000; Molis *et al.* 2006). Therefore, arthropods may respond positively, negatively or indifferently to allelochemicals activated by rodent grazing.

Plants can react to herbivory by compensatory growth, which is a form of tolerance strategy, when replacement for lost tissue is energetically more profitable than chemical defence (Meijden, Wijn & Verkaar 1988). There are studies which reported that compensatory growth was activated by rodent grazing (Elmqvist *et al.* 1987; Ericson & Oksanen 1987). The new re-growth structures may be positive for herbivores as they may contain less secondary compounds and increase palatability (Hjaltén, Danell & Ericson 1996; Sullivan & Howe 2011).

Changes in plant primary chemistry may have implications for arthropod communities too (Huberty & Denno 2006; White 1993, p.13). Herbivorous arthropod species are limited by nitrogen and phosphorus and depend on the income on plants. Rodents

selectively grazing on nutritious plants and plant parts with high nitrogen content may decrease mass of high forage quality for arthropods (Sirotnak & Huntly 2000). However, the negative effect is possibly counterbalanced by enhanced availability of chemical elements from faeces (Bardgett, Wardle & Yeates 1998; Clark *et al.* 2005).

It is assumed that as some plant resources will become unavailable due to undesirable changes in chemistry after rodent grazing, herbivorous species will be forced to search for new resources. Movements may expose them to higher risk of mortality by predators. Alternatively, they can keep feeding on modified tissues of less quality, which may lower their potential fecundity (Schult 1992). If a resource becomes limited, competition between herbivores may play a role as well (Speight, Hunter & Watt 2008, p. 106). Diversity and interactions within the arthropod community can also be influenced by re-growth structures in plants (Obermaier *et al.* 2008; Ohgushi 2008), which may provide additional forage and new habitat / oviposition opportunities (Ohgushi 2008). Decline of food resources with high nitrogen content due to selective feeding of rodents may have negative influence on the development of juveniles of arthropod populations (Speight, Hunter & Watt 2008, p.61 - 62). This effect is assumed to be mitigated by availability of nutrients from evenly redistributed faeces leading to higher mineralization rate (Mattson Jr 1980; Sirotnak & Huntly 2000). In addition, the quality of plant resources determines the functional role of arthropod omnivores, which in conditions of inferior plant resources switch to non-plant food or predatory mode (Janssen & Sabelis 2004).

The full role of arthropods for ecosystem functioning is not entirely recognized yet. So far they are acknowledged as an important component of biodiversity and of food webs, they work as dispersal agents distributing seeds, fungal spores or pollen, and they influence net primary productivity, microbial activity, decomposition and nutrient cycling (Weisser & Siemann 2004). Consequences of changes in populations of arthropods are believed to be reflected in ecosystem processes.

The objective of this thesis was to study whether and to what degree boreal forest rodents may indirectly affect arthropod communities through changes in density. I investigated arthropod communities under various rodent densities at first at the order level, and secondly, at the functional group level. In addition, I looked at early and late periods of the growing season. As an indicator I used abundance and biomass of arthropods. I expect that increased rodent density introduces potential changes in resource availability, which will have negative consequences for arthropod herbivores due to reduced plant quality and availability. This may lead to intensified competition

among phytophagous arthropods, resulting in reduced biomass or abundance. Increased movement in search of forage may benefit predators and result in increased biomass or abundance of predaceous arthropods. I expect the effect will be stronger later in the growing season, when rodent populations are more abundant.

2. Methods

2.1 BEcoDyn project

The work done for this thesis was part of the BEcoDyn project (the **B**oreal forest **Eco**system **Dyn**amics) at Hedmark University College, studying effect of vole population cycles on ecosystem dynamics of boreal forest. The design of this project created some constraints that might not have been present if my field work was specifically designed for my study. I refer to these constraints in the discussion part of the thesis (chapter 4.3).

2.2 Study area

The study area was situated in the forested area of the Glomma valley in Stor--Elvdal municipality, Norway (61°57′N 11°05′E, Fig. 1). It belongs to the middle boreal zone dominated by coniferous woodlands and mires. The boreal zone is characterized by short growing seasons and cold winters with snow cover persisting over a long period. In my study area, the growing season lasts approximately 150 days, beginning in the end of April and lasting until the end of September. Snow cover remains for around 175 days, from November to April (Moen 1999). Mean July temperature calculated for the period 2004 - 2014 was 15.5 °C. Mean January temperature for the same period was -9.1 °C. Mean annual temperature was 3 °C. Mean annual precipitations for the period 2003 – 2013 were 850 mm.

The summer 2014 when I collected the data was very warm with a prevalence of sunny days. The average temperatures for this summer with deviations from normal values (in brackets) from period 1961 - 1990, were following: June = 12.7°C (- 0.3), July = 17.9 °C (+ 3.9), and August = 13.2°C (+ 0.7). Precipitations for the summer 2014 were as follow: June = 66.1 mm (- 12), July = 79 mm (- 11), and August = 110.3 mm (+ 30).

Values for temperature were obtained from the meteorological station at Evenstad, which is situated within the study area. For precipitations I used records from station Rena – Haugedalen, about 15 km southeast from the study area. This station is the closest to the study area to provide data on precipitation (Norwegian Meteorological Institute 2015). The study was carried out in forest habitats of different age classes including clear-cuts, young and old forest stands in six different localities of 4 km^2 (Figure 1).
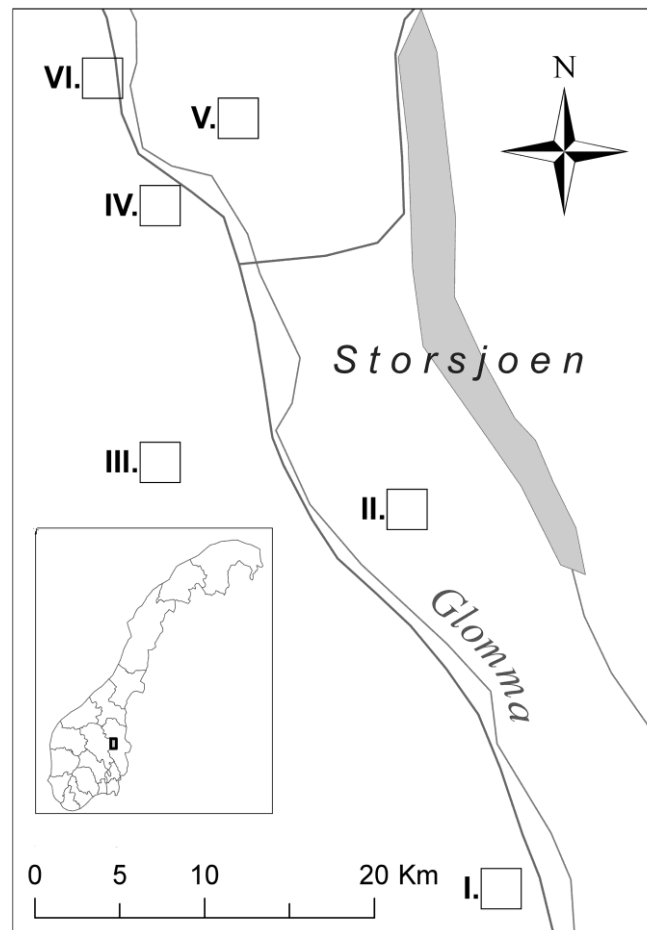
Figure 1: Position of the six sampling localities (□) within the study area in Stor-Elvdal municipality. The municipality is part of Hedmark County, Norway (inlet).

2.3 Data collection

2.3.1 Capturing rodents

Rodents were captured in June, July and September 2014 in a parallel study by David Carricondo Sánchez. Each locality contained four trapping grids, each consisting from 16 Ugglan traps (multiple-capture live-traps). Arrangement of traps within a grid and position of grids within the localities is showed in Figures 2 and 3. The grids were distributed randomly in bank vole (*Myodes glareolus*) habitat (bilberry forest). Consequently the largest proportion of captures constituted of bank voles, followed by field voles (*Microtus agrestis*). Within other forest habitats which were used to sample arthropods, grey-sided voles

(*Myodes rufocanus*) and wood mice (*Apodemus sylvaticus*) may also occur (Ecke, Lofgren & Sorlin 2002; Gorini 2010; Panzacchi *et al.* 2010).

Trapping was performed once a month during four days. The first day in the morning traps were filled with a lure - oats and carrots, followed by first control in the afternoon. On the second and third day traps were controlled twice – in the morning and in the afternoon. The last control was done on the morning of the fourth day. Captured rodents were marked by fur clipping to identify recaptured individuals. The season 2014 was a peak year for vole populations (Kaja Johnsen, Hedmark University of Applied Sciences, personal communication).
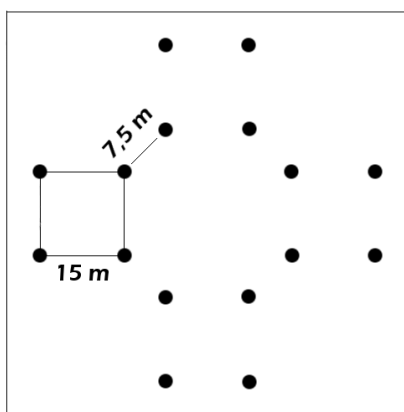
Figure 2:
Placement of 16 rodent traps (●)
within a trapping grid.
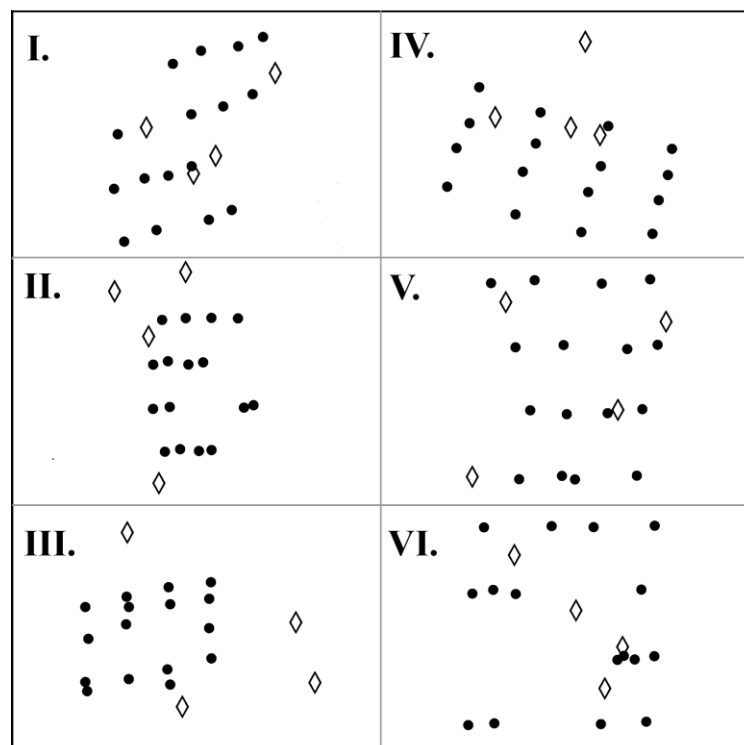
Figure 3: Organization of rodent trapping grids (◊) and insect sampling plots (●) within the six sampling localities in Stor-Elvdal municipality, Norway.

2.3.2 Sampling arthropods

Arthropods were sampled on 16 plots within each locality (Fig. 3), resulting in a total of 96 sampling plots. The plots were bound to vegetation sampling plots of the size 1x1 m used to sample vegetation in BEcoDyn project. They were evenly distributed along four parallel lines, which were 500 m apart covering 1.5 km^2 within the core area of the sampling localities. Each line comprised four plots. The distance between consecutive plots on the line was 250 m and it varied according to terrain conditions (e.g., steep slopes were avoided). I collected arthropods from dwarf shrubs (e.g., graminoids, herbs, shrubs, ferns) and ground vegetation layer (e.g., mosses, lichens) by using a sweeping net. Placed at the center of 1 m^2 sampling plots I took six sweeps to the four perpendicular directions, in total 24 sweeps per plot (Figure 4). The directions were adjusted to surrounding vegetation. I gathered arthropods into small plastic tubes at each plot without using alcohol, and labelled them with plot code, date and time. The samples were taken to the lab where I proceeded to further identification.

Sampling was performed in June and August 2014 in order to survey the arthropod community representative for early and late growing season. In August, instead of 96 plots only 95 were sampled, as one plot in *locality IV* lost its marking from June. To reduce sampling error, it was important to eliminate variation in arthropod activity due to various weather conditions (Williams 1940; Abdullah 1961; Taylor 1963; Speight, Hunter & Watt 2008). Therefore I collected samples only during days with homogeneous, favourable weather with sunshine, little wind and without rainfall.
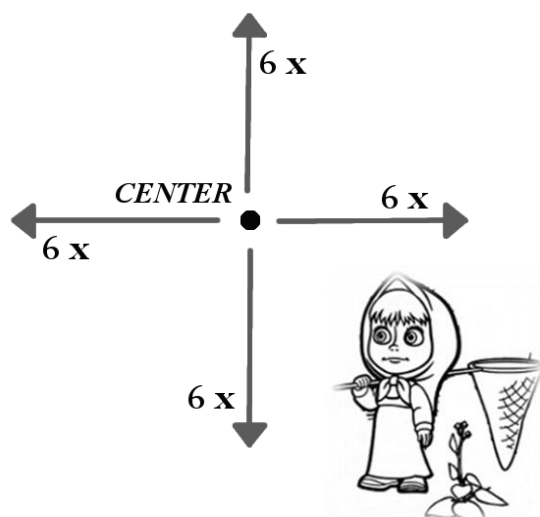
Figure 4:
Outline of the method I used in sampling the arthropods. Four pointing arrows represent four perpendicular directions, in which I took 24 sweeps (6 sweeps in each direction) from the plot center.

2.3.3 Laboratory work

In the laboratory, I cleared the samples of the vegetation, then sorted them into the different orders (Triplehorn & Johnson 2005) and stored them in 95% ethanol in Ephendorf tubes. I counted number of individuals per order for each plot. Afterwards, I measured similarly biomass by weighing dry samples. Samples were dried at 60°C for 24 hours. To weigh them, I used a scale with an accuracy of 0.1 mg. As the process of drying can corrupt the samples, it was necessary to identify taxonomy before drying.

2.4 Statistical analyses

2.4.1 Predictor variables

The predictor of main interest in this study was **rodent population density**. I used minimum number alive (MNA) calculated for months June and August in order to coincide in time with sampling of arthropods. I estimated MNA for each trapping grid. For MNA in June, I used data on captures from June. To estimate August population, I interpolated MNA calculated for July and September. For each arthropod sampling plot I assigned a value representing rodent density from the closest trapping grid. This was done in ArcGIS 10.1 (ESRI 2011).

Further I included **vegetation** as it is a primary determinant of arthropod abundance, defining habitat and food resources available for herbivorous arthropods (Price 1992). I specified five fundamental vegetation types, two of them with two subcategories:

1. ***pine forest***   a) *with lichens*,   b) *with dwarf shrubs*
2. ***bilberry forest***
3. ***ferns – shrubs forest***
4. ***swamp vegetation***
5. ***clear-cut***   a) *poor clear-cut*,   b) *rich clear-cut*

The categories are based mostly on characteristic of bottom and field layer. In the description I followed Fremstad (1997) and Johansen, Aarestad and Øien (2009), and the description is attached in Appendix A. The categories exhibit various plant species composition, richness and plant biomass. There are also perceptible differences in moisture level.

Several environmental and habitat conditions, such as temperature, humidity in the air or exposure to sunshine, influence arthropods performance and activity. These were considered in the analyses as following:

To take into account **circadian shifts** in humidity and temperature, I specified three categories – *morning*, *day* and *evening*. Humidity falls to the lowest values during day, increases towards sunset, and highest saturation is at sunrise. With increasing temperature, humidity decreases, and vice versa (Williams 1940). As *day* category I considered the part of the day from 10 to 18 o'clock (GMT + 2 hours). With lower temperature and higher humidity, category *morning* was considered until 10 o'clock. Similarly, *evening* was after 18 o'clock.

In ArcGIS I calculated the amount of radiant energy received by each plot. **Solar radiation** is given by topography. It is a conjunct effect of elevation, aspect, slope and hillshade. Values were calculated for the months June and August.

Although UV irradiance correlates positively with altitude because of the decreased amount of absorbers in higher altitude, temperature with increasing altitude decreases. Therefore, in addition to solar energy I decided to include single effect of **altitude**.

Exposure of bottom layer to sun is also given by **shade** from canopy cover. It influences heat and moisture level in the layer. In the field, I estimated proportion of shade for each sampling plot. I used three categories: *< 20 % shade*, *20 – 80 %* and *> 80 % shade*.

The numbers of plots for the factor levels of the categorical variables (*vegetation types*, *part of the day*, *shade*) are listed in the Table 1.

Table 1: Distribution of the factor levels of the categorical predictors (*vegetation type*, *shade*, *part of the day*) in the data, expressed by number of plots representative for the factor level. The table considers total number of plots = 96. The categories of the variable *part of the day* are distributed differently in June and in August, as the day in August is shorter than in June. The plot missing in August was represented by *rich clear-cut* with *< 20 % of shade*.

Predictor	*Factor*	*Nr. of plots*	
	Pine forest with lichens	10	
	Pine forest with dwarf shrubs	6	
Vegetation	Bilberry forest	34	
types	Fern – shrub forest	20	
	Swamp vegetation	4	
	Poor clear - cut	13	
	Rich clear-cut	9	
	< 20 %	40	
Shade	20 – 80 %	41	
	> 80 %	15	
		June	*August*
Part	morning	4	5
of the day	day	62	76
	evening	30	14

2.4.2 Multivariate analyses using Canoco

In order to describe patterns in insect communities and measured environmental variables, and to find out whether there is a relationship between rodents and distinct arthropod orders, I performed ordinations in Canoco 5.0 (Braak & Šmilauer 2012) separately for June and August. As a response I used abundances of arthropods per orders and plot. Orders collected in sampling are listed in Table 1. Based on the value of the longest gradient in detrended correspondence analysis (DCA), with downweighted rare orders (value in June = 2.0, in August = 2.13), I decided to use linear methods (Šmilauer & Lepš 2014, p. 27 - 28). Given that linear methods do not allow to downweight rare orders (Šmilauer & Lepš 2014, p. 30), I excluded orders observed ≤ 6 plots from the further analyses. These were orders Dermaptera, Neuroptera and Plecoptera, which I excluded from both months, and in addition to that I excluded Psocoptera from June and Trichoptera from August (see Table 2). I first performed unconstrained partial principal component analysis (PCA) to investigate the patterns in arthropod community. I then used constrained partial redundancy analysis (RDA) with forward selection to investigate the relationship between abundance of orders and environmental variables. *Locality* (Figure 1) was included as a covariable in both analyses. The decision on partial analyses (including covariables) was based on the result of RDA with forward selection, where *locality* emerged in both months as significant. Because of the high numbers of environmental variables, in particular categorical variables, it was necessary to determine a parsimonious set of significant predictors. Therefore, I also present only significant environmental variables in RDA diagrams, and likewise, only these significant environmental variables were presented as supplementary variables in PCA diagrams. The variables were considered significant when $p < 0.05$. The p-values were adjusted by false discovery rate (Šmilauer & Lepš 2014, p. 91). In case of a significant factor level of a categorical variable, I included all factor levels within that variable in the RDA. In all analyses, four ordination axes were calculated. Axes constrained by explanatory variables were tested for significance by 499 unrestricted Monte Carlo permutations, and p-values stated in the result section refer to this test.

2.4.3 Analyses of biomass using linear regression models

I used programs R 3.1.1 (R Core Team 2014, http://www.R-project.org/) and R Studio to analyze biomass of arthropods. I grouped orders according to their membership to a particular feeding guild into *herbivores* and *predators* (Triplehorn & Johnson 2005;

Chinery 2007). However, several orders comprised species which differ in their feeding habits. These were consequently merged into *mixed group*. The orders with corresponding functional group are listed in Table 2. I did not include in the analysis orders Plecoptera and Trichoptera, as adults mostly do not feed and their nymphal / larval stages are aquatic (Chinery 2007).

Table 2. List of arthropod orders collected during field sampling with an overview of functional groups, their abundance (number of individuals) and occurrence (number of plots the order was present) in the months June and August. Total number of plots was in June = 96, in August = 95.

ORDER (Latin)	ORDER (English)	FUNCTIONAL GROUP	JUNE		AUGUST	
			Abundance	Occurrence	Abundance	Occurrence
Acari	mites	mixed	605	70	1725	94
Araneae	spiders	predators	169	75	383	78
Coleoptera	beetles	mixed	60	43	45	35
Collembola	springtails	mixed	1393	92	7215	95
Dermaptera	earwigs	mixed	0	0	1	1
Diptera	true flies	mixed	2964	94	979	92
Hemiptera	bugs	herbivores	624	80	1808	90
Hymenoptera	ants, wasps, bees	mixed	438	91	899	93
larvae	-	herbivores	119	55	20	19
Neuroptera	ant-lions, lacewings	predators	0	0	5	4
Opiliones	harvestmen	predators	8	7	7	6
Plecoptera	stoneflies	-	6	4	1	1
Psocoptera	psocids	herbivores	3	1	98	47
Thysanoptera	thrips	mixed	76	40	31	19
Trichoptera	caddisflies	-	61	19	2	2

I applied linear mixed models using the "lme" function under the package *nlme* to analyze how arthropod biomass in different functional groups responded to rodent density, vegetation types, elevation, solar radiation, shade and different time of the day. Similarly as in Canoco analyses, I conducted separated analyses for June and for August, as the pairs-function showed that the variables *month* and *rodents* were highly correlated (correlation coeficient = 0.89). By using simple models, I inspected whether the relation of response variable to the numerical predictors was linear or non-linear. Similarly, I inspected whether there were possible interactions between predictors and *functional groups* of arthropods. As the distribution of response variable (biomass of arthropods) was skewed, I logarithmically

transformed the variable (log + 1 to account for zeros) to comply with the assumption of a normal distribution of the response variable. In model selection I followed Zuur *et al.* (2009). I first evaluated the random component by testing the effect of *locality*, *rodent trapping grid ID* and nested effect of *rodent trapping grid within locality* as a random intercept. These models were compared with "gls" models under restricted maximum likelihood (REML). For model selection of the random component I used the Akaike's information criterion (AIC). I used AIC also in determining the fixed component and in selecting the ultimate model. Here I applied the maximum likelihood (ML) estimation. The model with lowest AIC value was considered as the best model (Burnham & Anderson 2004). To provide support for selected model I calculated ΔAIC (information loss compared to the best model) and AIC*w* (weight of evidence expressed as probability). In case of equally good models (ΔAIC ≤ 2)(Burnham & Anderson 2004), I followed the principle of parsimony and selected the model with the lowest number of predictors. Overall, I tested 40 models for each month. Goodness-of-fit of the final model I interpreted as marginal (variance explained by fixed factors) and conditional (variance explained by both – fixed and random factors) effect, which I estimated by using package *MuMIn*. In addition to simple effects of the predictors (*rodents*, *vegetation types*, *elevation*, *solar radiation*, *shade*, *part of the day*), I included in the models interactions between *functional group* and the variables: *rodents*, *vegetation*, *elevation*, *part of the day* and *shade*. To plot the results I used function *predict*.

3. Results

3.1 Multivariate analyses using Canoco

Patterns within arthropod community in month June are displayed in the ordination diagram of partial PCA (Figure 5), together with supplementary variables − *rodents*, *shade* categories and *vegetation types*. The first two axes explained together 80.0 % of the variation (eigenvalue 1 = 0.45, eigenvalue 2 = 0.14, Table 3). However, correlation of the axes with environmental variables was not particularly strong (Table 3; pseudo-canonical values).

The first principal component was negatively correlated with *rodents*, and factor levels *>80 % shade*, *swamp vegetation* and *pine forest with lichens*, and positively with *ferns-shrubs* forest type (Figure 5). The second axis was primarily correlated positively with *bilberry forest* and negatively with *poor clear-cut*. Positions of the vegetation types *pine forest with dwarf shrubs* and *rich clear-cut*, which were further from the origin and asymmetrical compared to other factor levels, indicating the unbalance in the data and their lower frequency. Several arthropod orders within the diagram fell close to the origin, what means they are not well characterized by the two displayed axes. These were orders Thysanoptera, Opiliones, Trichoptera, Hymenoptera, Araneae and larvae. On the other hand, the orders that show a relationship with the axes were Diptera, Collembola, Acari, Coleoptera and Hemiptera. *Rodents* were represented only by short arrow, what suggested that they did not have very strong effect on the arthropod community. Hemiptera showed a positive association with *rodents*, while Diptera showed strong negative association with *rodents*, followed by Collembola. Coleoptera and Acari were not related to *rodents*. Regarding the mutual relationships between arthropods, Acari showed a positive correlation with Coleoptera, which were also in weaker positive correlation with Collembola. Diptera showed a strong negative correlation with Hemiptera, which stand in opposition in the diagram (Figure 5). The same relationship applies to associated factor levels − shaded areas (*>80 %*) and several vegetation types (*rich clear-cut*, *swamp vegetation*, *pine forest with lichens*) positively associated with Hemiptera, were negatively associated with Diptera, and the other way around. Diptera was clearly the only order with a positive relation to *ferns-shrubs forest* and *pine forest with dwarf shrubs*. Group of orders Coleoptera, Acari and Collembola was positively associated with *bilberry forest*. These orders, together with Diptera, were in positive association with intermediate shade (*20 – 80 %*).

Table 3. Results of partial PCA performed for June, summarizing eigenvalues, explained variation and additional statistics for each of the four computed ordination axes.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4540	0.1480	0.0873	0.0512
Explained variation (cumulative)	60.36	80.03	91.63	98.44
Pseudo-canonical correlation (suppl.)	0.5200	0.2495	0.3617	0.6303
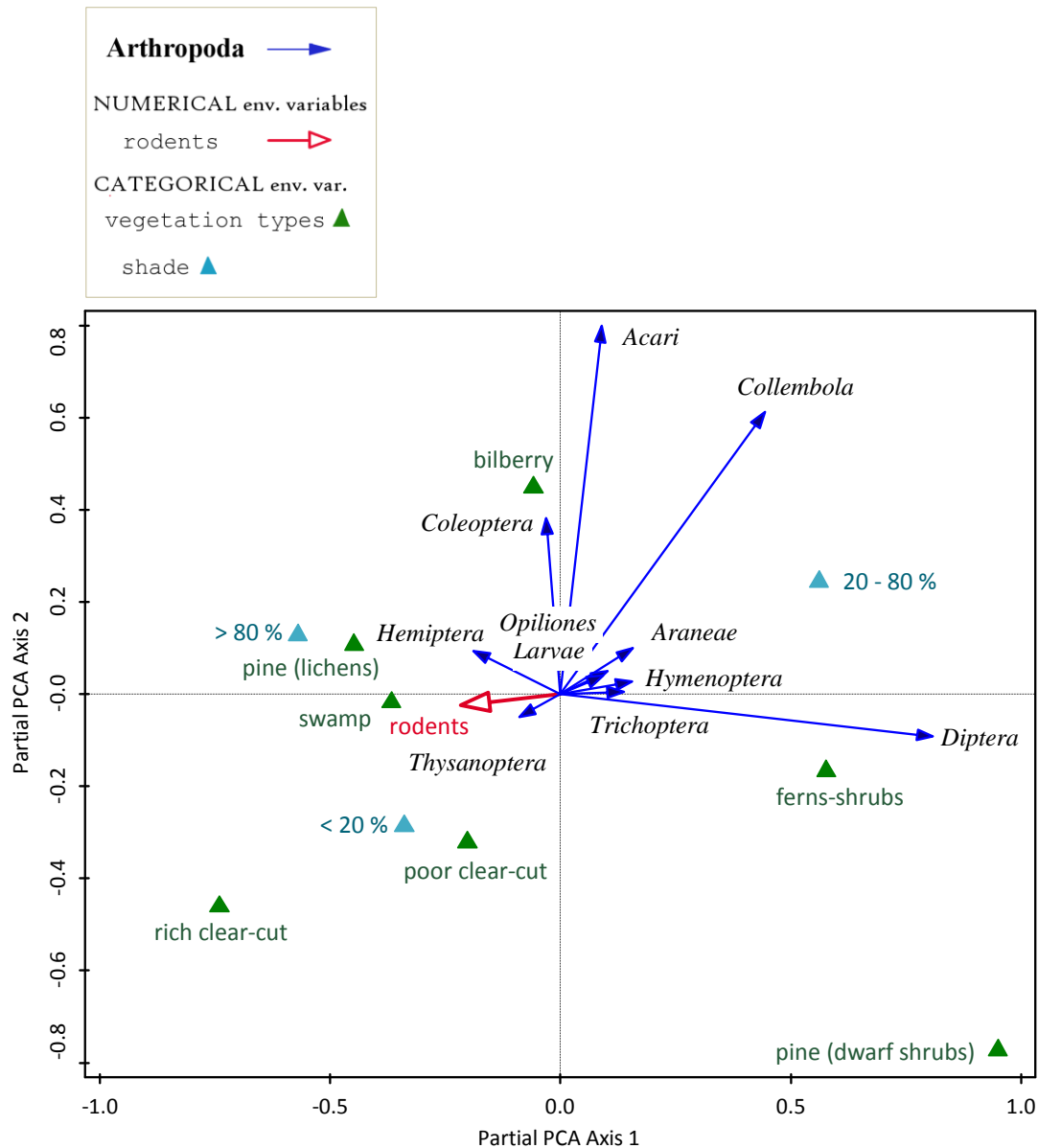
Figure 5. Partial PCA biplot with axes 1 and 2, displaying arthropod orders and supplementary variables (*shade*, *rodents* and *vegetation types*) in June.

In the month of June *shade*, *rodents* and *vegetation types* were determined by partial RDA with forward selection as significant explanatory variables explaining best the variance in arthropod abundance (Table 4). The first two axes explained 19.5% of the variation (p = 0.004; Table 5). However, the first axis alone explained more than 16 % (eigenvalue = 0.12), and all higher axes explained much less (see eigenvalues; Table 5). These results are reasonable, given that all measured explanatory variables together explained 25.4 % of the variation (p = 0.01). The low percentage of variance explained by the first axis in this analysis (16.6 %) compared to 60.4 % explained by the first axis in unconstrained analysis (Table 3) suggests there is a lot of variability in arthropod data which cannot be attributed to the used explanatory variables.

Table 4: Significant environmental variables determined by forward selection using Monte Carlo permutations in RDA in June – *shade* categories, *rodents* and factors of *vegetation types*, with percentages of explained variation and contribution, and with values of pseudo-F statistics and p-values.

Variable	*Explains %*	*Contribution %*	*pseudo-F*	*P*
20 – 80 % shade	**5.9**	**23.2**	**5.6**	**0.002**
< 20 % shade	0.4	1.5	0.3	-
> 80 % shade	0.4	1.5	0.3	-
Rodents	**5.1**	**20.2**	**5.0**	**0.014**
Ferns – shrubs forest type	**4.5**	**17.5**	**4.6**	**0.014**
Pine f. - dwarf shrubs	2.3	9.2	2.4	-
Swamp vegetation	1.7	6.5	1.7	-
Pine f. - lichens	1.1	4.3	1.1	-
Bilberry forest	0.5	1.9	0.5	-
Rich clear-cut	0.5	2.2	0.6	-
Poor clear-cut	0.5	2.2	0.6	-

Table 5: Results of partial RDA performed for June, summarizing eigenvalues, explained variation and additional statistics for each of the four computed ordination axes.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.1250	0.0216	0.0118	0.0060
Explained variation (cumulative)	16.61	19.48	21.05	21.85
Pseudo-canonical correlation	0.5293	0.5293	0.3773	0.2141
Explained fitted variation (cumulative)	75.72	88.80	95.95	99.58

The ordination diagram of partial RDA with axes constrained by significant environmental variables from Table 4 displays how were arthropods related to these variables (Figure 6). Axis 1 was negatively correlated with *rodents*, factor levels *>80 % shade*, *poor clear-cut* and *pine forest with lichens*, and positively with *ferns-shrubs forest* vegetation type, similarly as in unconstrained analysis. Axis 2 was mainly correlated negatively with *bilberry forest*, and positively with *swamp vegetation* and *rich clear-cut*. In this case, because the analysis was constrained, the effect of *rodents* seemed to be stronger. Associations with shade categories and vegetation types were slightly different too. None of the orders showed in immediate, strong positive association with *rodents*. Hemiptera, and also Thysanoptera and Opiliones were only weakly related. The negative correlation of Diptera and Collembola (with *rodents*) corresponded to the unconstrained analysis (Figure 5). Hemiptera was positively correlated with unshaded areas (*<20 %*) and mainly with *swamp vegetation* and *rich clear-cut*. In positive association with these factor levels were also Trichoptera and Thysanoptera. According this analysis, not only Diptera, but also Collembola was associated with *ferns-shrubs* forest type and *pine forest with dwarf shrubs*. Most of the orders were associated with intermediate shade *20 – 80 %* (Diptera, Collembola, larvae, Acari, Opiliones). Larvae, Acari and Opiliones were primarily related to *bilberry forest* (Figure 6).
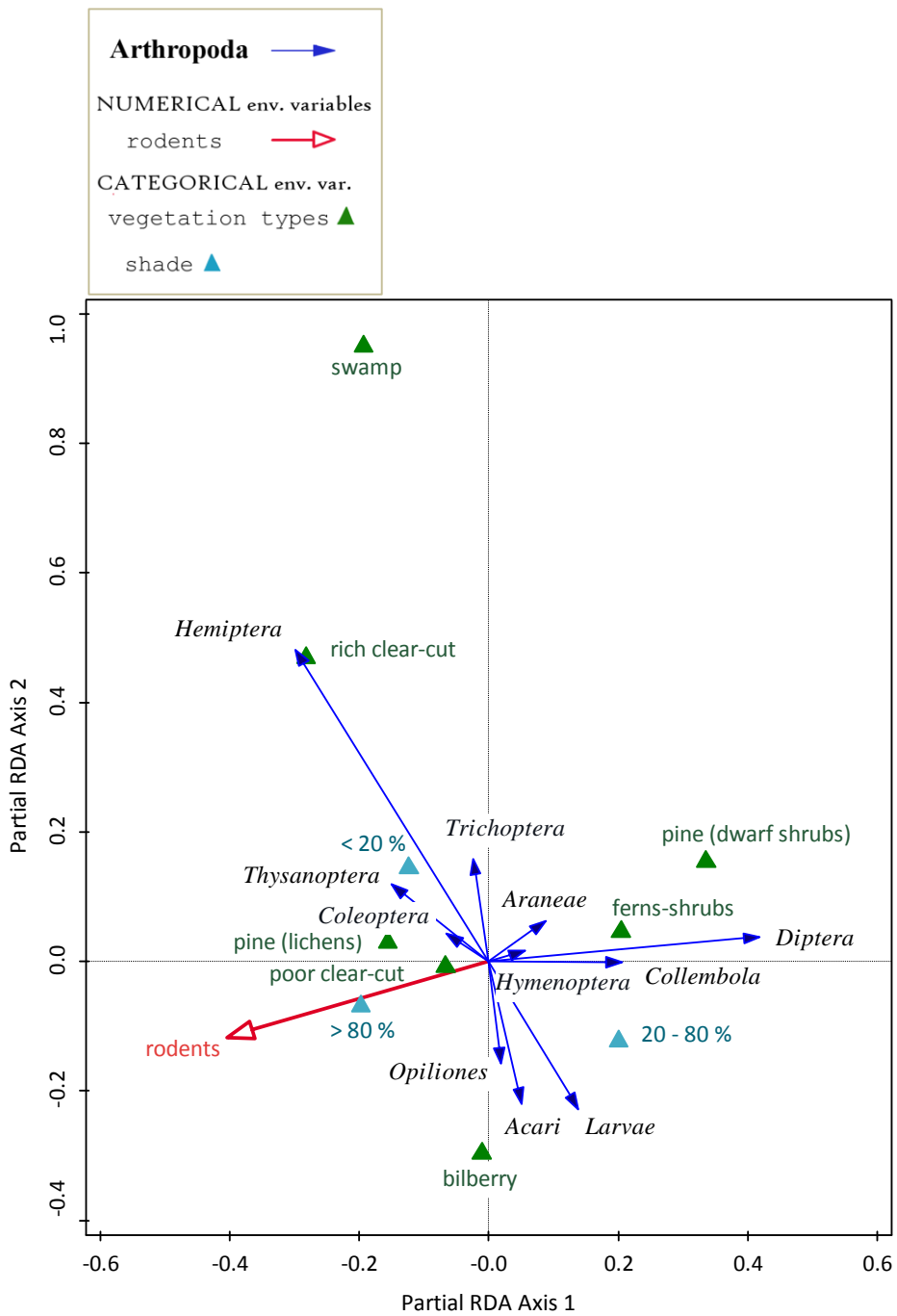
Figure 6: Partial RDA ordination biplot with axes 1 and 2, displaying arthropod orders and significant explanatory variables (*shade*, *rodents* and *vegetation types*) in June.

The ordination diagram of partial PCA on Figure 7 displays patterns within arthropod community in August, together with supplementary variables - *vegetation types*, *part of the day* and *elevation*. The first axis explained 80.5 % of the variation (eigenvalue 1 = 0.68), what is far more than explained by the other three axes (Table 6).

Axis 1 was primarily correlated with vegetation types – positively with *bilberry forest*, and negatively with *poor clear-cut* and *swamp vegetation*. Axis 2 was mainly positively correlated with *ferns-shrubs* forest, and negatively with *evening*. Positively correlated with second axis was also *elevation*, which however showed very weak effect. Majority of the orders was in mutual positive association – particularly Collembola with Araneae, which arrows overlap, followed in descending trend by Opiliones, Psocoptera, Diptera, Hymenoptera and Acari. All these orders adhered to *bilberry forest* and avoided *pine forests*. Collembola and Araneae were negatively correlated with Thysanoptera, which was in positive relationship with Hemiptera and Coleoptera. Thysanoptera related to *clear-cuts* and *pine forests*, while Hemiptera and Coleoptera to *rich clear-cut*. Hemiptera and Coleoptera were in positive association also with some of the orders from the earlier mentioned cluster, specifically with Acari, Hymenoptera, Diptera. They were all associated with *evening*. *Morning* category was placed in the outskirts of the ordination space what means it is less frequent in the data. With *morning* was positively associated couple Collembola and Araneae, and negatively Hemiptera and Coleoptera (Figure 7).

Table 6: Results of partial PCA performed for month August, summarizing eigenvalues, explained variation and additional statistics for each of the four computed ordination axes.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.6810	0.0823	0.0650	0.0122
Explained variation (cumulative)	80.50	90.24	97.92	99.36
Pseudo-canonical correlation (suppl.)	0.6878	0.5106	0.5600	0.5022
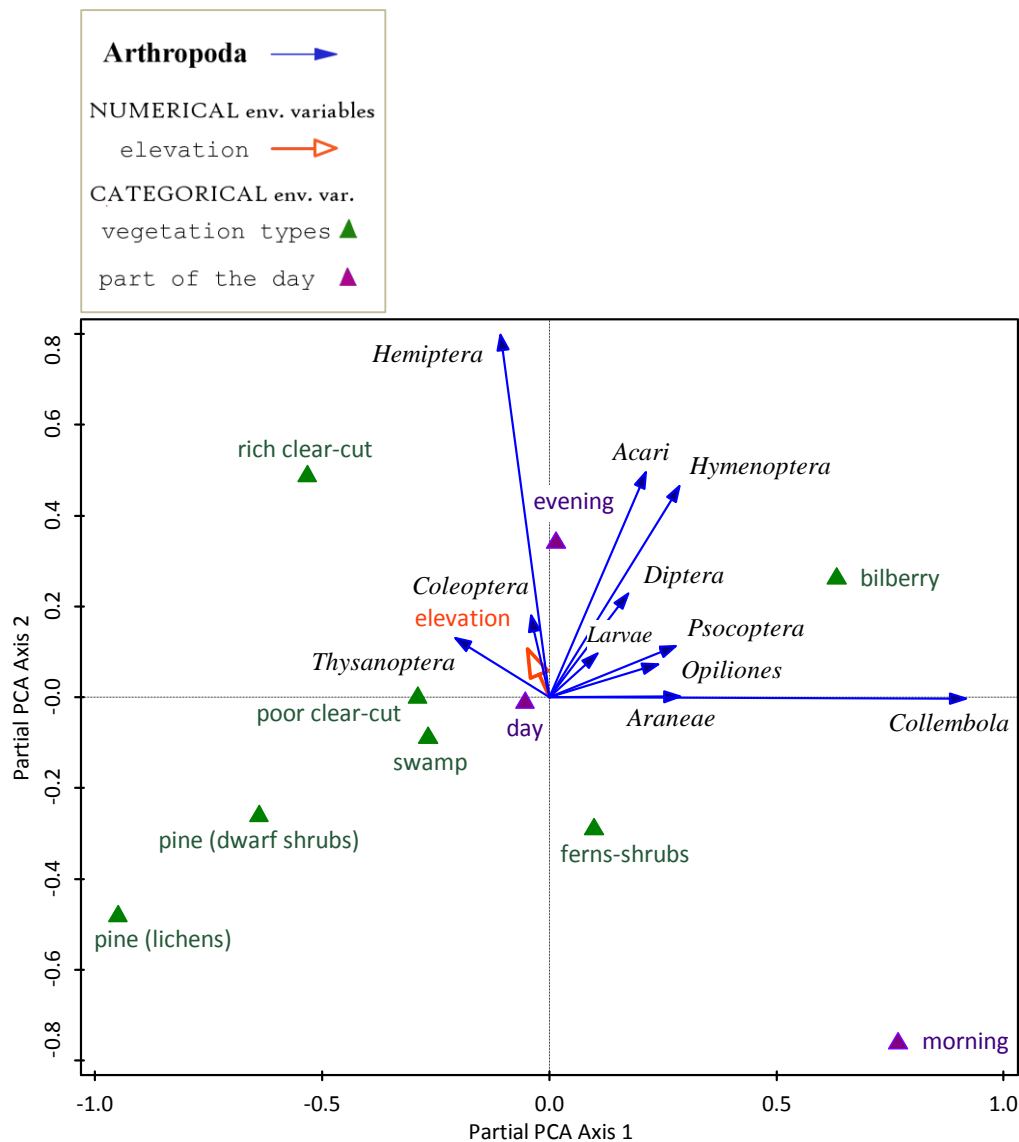
Figure 7: Partial PCA biplot with axes 1 and 2, displaying arthropod orders and supplementary variables (*vegetation types*, *part of the day* and *elevation*) in August.

Significant predictors determined by forward selection of partial RDA in month August are summarized in Table 7. However, now *rodents* and *shade* were not included as in June. Variables that explained best the variation in the arthropods were *vegetation*, *part of the day* and *elevation*. In particular, a lot of variance explained factor level *bilberry forest* (22.5 %, p = 0.002, Table 6).

In this analysis, the first axis explained 38.2 % of the variation (eigenvalue 1 = 0.32, Table 8), and as it is showed in Table 8, the eigenvalues and the variation explained by other three axes lowered dramatically. The result is good compared to 46.4 % explained when all measured explanatory variables were used (p = 0.002). Still, there was a big difference in

variation explained by axis 1 in constrained analysis (38.2 %, Table 8) and axis 1 in unconstrained analysis (80.5 %, Table 6). Therefore, similarly as in June, a lot of variability in response data cannot be attributed to the used explanatory variables.

Table 7: Significant environmental variables determined by forward selection using Monte Carlo permutations in RDA in August – factors of *vegetation types*, *part of the day* and *elevation*. Displayed are percentages of explained variation and contribution, and with values of pseudo-F statistics and p-values.

Variable	Explains %	Contribution %	pseudo-F	P
Bilberry forest	**22.5**	**48.4**	**25.5**	**0.002**
Pine f. – lichens	5.7	12.3	6.9	unknown
Ferns – shrubs forest type	3.2	6.8	4.0	unknown
Rich clear-cut	0.4	0.9	0.5	unknown
Pine f. – dwarf shrubs	0.9	1.9	1.1	unknown
Swamp vegetation	0.3	0.6	0.3	unknown
Poor clear-cut	0.3	0.6	0.3	unknown
Part of the day – morning	**6.4**	**13.8**	**8.6**	**0.004**
Part of the day – day	1.6	3.5	2.2	unknown
Part of the day – evening	1.6	3.5	2.2	unknown
Elevation	**2.6**	**5.6**	**3.7**	**0.04**

Table 8: Results of partial RDA performed for August, summarizing eigenvalues, explained variation and additional statistics for each of the four computed ordination axes.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.3233	0.0220	0.0189	0.0031
Explained variation (cumulative)	38.22	40.82	43.05	43.42
Pseudo-canonical correlation	0.6902	0.5282	0.5189	0.5063
Explained fitted variation (cumulative)	87.91	93.89	99.03	99.88

Figure 8 displays the ordination diagram of partial RDA, with axes constrained by significant environmental variables (*vegetation types*, *part of the day*, *elevation*; Table 7). The correlation of the variables with the axes was almost identical to the unconstrained analysis (Figure 3). The only exception was factor level *evening*, which in this analysis lies in the origin. It means that the arthropod orders occurred in average abundances. Constrained analysis intensified the effect of *elevation*, which was demonstrated by longer arrow. Responses of the arthropods showed pattern similar to the unconstrained analysis too. The diagram revealed there was a correlation between *elevation* and *rich clear-cut*, what

probably influenced also the positive association of Hemiptera with *elevation*. The other orders seemed to be only weekly related or unrelated to *elevation*. Associations with vegetation types and with *morning* category coincided with unconstrained analysis, except for Coleoptera which was not well performed in this analysis (too short arrow).
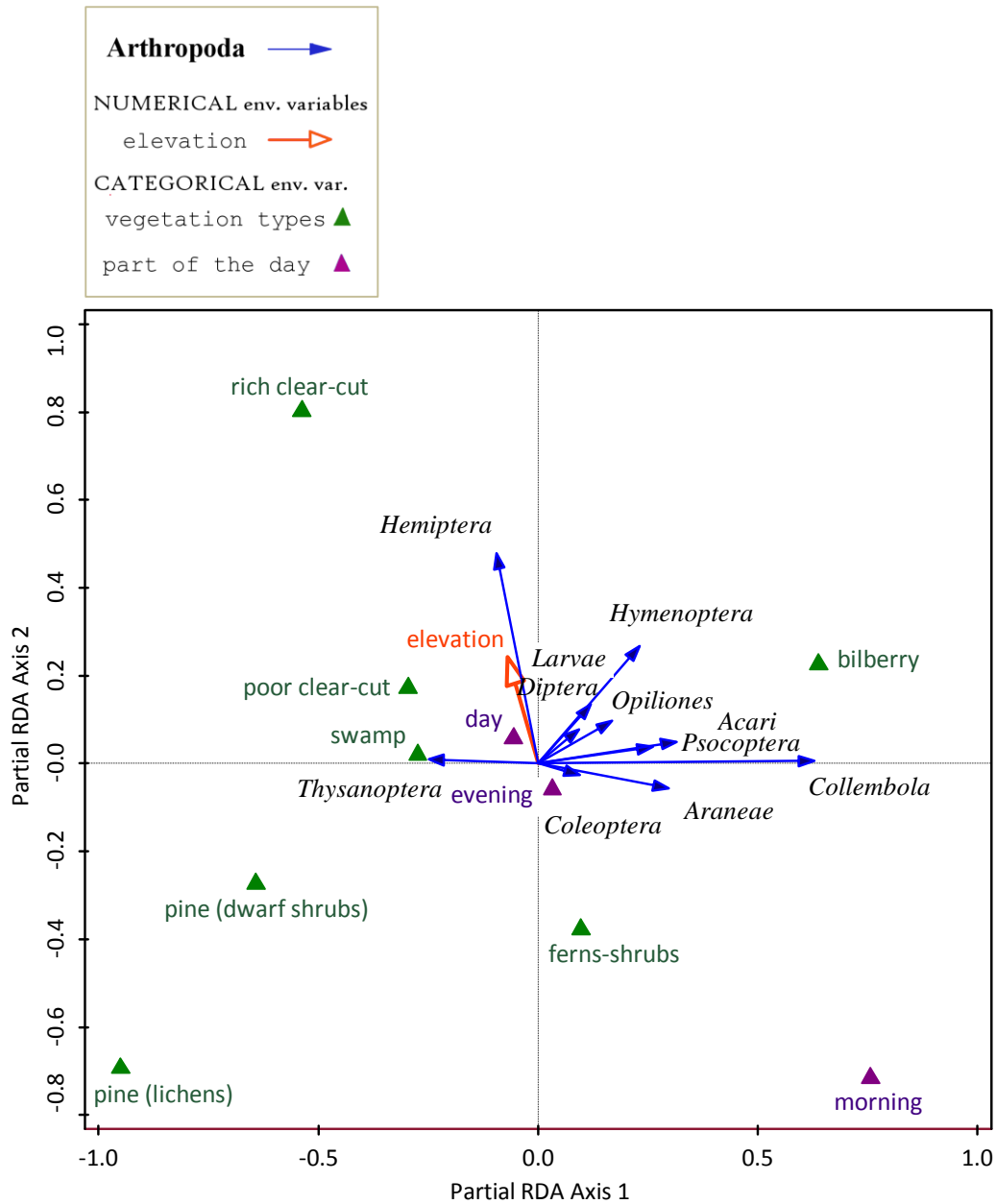
Figure 8: Partial RDA ordination biplot with axes 1 and 2, displaying arthropod orders and significant explanatory variables (*vegetation types*, *part of the day* and *elevation*) in August.

3.2 Analyses of biomass using linear regression models

Locality was used as a random component in the mixed linear regression models in both months, in order to be consistent and to compare the outputs of the models. According to AIC, it was the best model in August. In June the model had similar AIC value to the model without random component.

In June, the model with the lowest AIC value included *rodents*, *vegetation*, and two interactions - *functional group*elevation* and *functional group*part of the day* (Table 9). Marginal effect of the model was $r^2 = 0.30$, and conditional effect was $r^2 = 0.33$.

Table 9: Model selection according to AIC (ΔAIC and AIC weight) in June. The response variable is biomass of arthropods per sampling plot and functional groups. Table contains 10 terminal models out of 40 tested models with degrees of freedom (df) and corresponding AIC values. Models are displayed in descending order, starting with the best model on top. Interactions between predictor variable and *functional group* are denoted by symbol (*) in model formula.

Model	df	AIC	Δ AIC	AIC weight
Rodents, Vegetation, Elevation*Func., Part.of.day*Func.	21	651.99	0	0.39
Solar rad., Rodents, Vegetation, Elevation*Func., Part.of.day*Func.	22	653.11	1.13	0.22
Shade, Rodents, Vegetation, Elevation*Func., Part.of.day*Func.	23	653.61	1.63	0.17
Rodents, Elevation*Func., Part.of.day*Func.	15	655.23	3.24	0.08
Rodents, Vegetation, Elevation*Func.	15	655.76	3.78	0.06
Vegetation, Elevation*Func., Part.of.day*Func.	20	657.17	5.18	0.03
Solar rad., Vegetation, Elevation*Func., Part.of.day*Func.	21	657.57	5.58	0.02
Shade, Vegetation, Elevation*Func., Part.of.day*Func.	22	658.37	6.38	0.02
Vegetation, Rodents*Func., Elevation*Func.	17	658.92	6.94	0.01
Elevation*Func., Part.of.day*Func.	14	660.42	8.43	0.006

Biomass of arthropods in June was negatively related to *rodents* (Table 10), however, the interaction between rodents and the functional group did not increase model fit (Table 9). As it is displayed on Figure 9, all arthropod functional groups (herbivores, predators, mixed group) responded in the same way to increasing rodent density by a decline in biomass.

Vegetation was important in determining biomass of arthropods (Table 10). Compared to *pine forest with lichens*, biomass sampled in vegetation types *swamp vegetation* and *rich clear-cut* was considerably higher. Biomass of herbivores and mixed group increased with elevation, while predators decreased (Figure 9). It also seems the

functional groups varied in activity according to the time of the day. The result indicates that the activity of herbivores and predators subsided during the evening hours (Table 10).

Table 10: Summary table from the selected final model in June which was used to explain variation in biomass of arthropods. Table displays log-transformed estimates with standard errors (SE), degrees of freedom (df), and t- and p-values for numerical predictors and for each factor level within a categorical variable, meaning general effect on the biomass of arthropods. In case of interactions, values are specified for the functional group. Part of the intercept are following factor levels – *pine forest with lichens* (vegetation type), *mixed group* (functional group) and *day* (part of the day). The estimates of other factors are relative to the intercept.

	Estimate	*SE*	*df*	*t-value*	*p-value*
Intercept	0.33690	0.37829	264	0.89	0.37
Pine forest (dwarf shrubs)	0.12591	0.22054	264	0.57	0.57
Bilberry forest	0.20526	0.15246	264	1.35	0.18
Ferns – shrubs forest	0.20749	0.16617	264	1.25	0.21
Swamp vegetation	0.51847	0.25460	264	2.04	0.04
Poor clear-cut	0.04577	0.18671	264	0.25	0.81
Rich clear-cut	0.63477	0.20051	264	3.17	0.002
Rodents	-0.03976	0.01523	264	-2.61	0.009
Elevation	0.00149	0.00064	264	2.34	0.02
Herbivores	-0.05232	0.43783	264	-0.12	0.91
Predators	0.41045	0.43783	264	0.94	0.35
Morning	0.52364	0.16665	264	3.14	0.002
Evening	0.32795	0.39404	264	0.83	0.41
Elevation : Herbivores	0.00022	0.00074	264	0.30	0.77
Elevation : Predators	-0.00180	0.00074	264	-2.44	0.02
Herbivores :Evening	-0.79275	0.22500	264	-3.52	0.0005
Predators : Evening	-0.70301	0.22500	264	-3.12	0.002
Herbivores : Morning	-0.48557	0.53563	264	-0.91	0.37
Predators : Morning	-0.45166	0.53563	264	-0.84	0.40
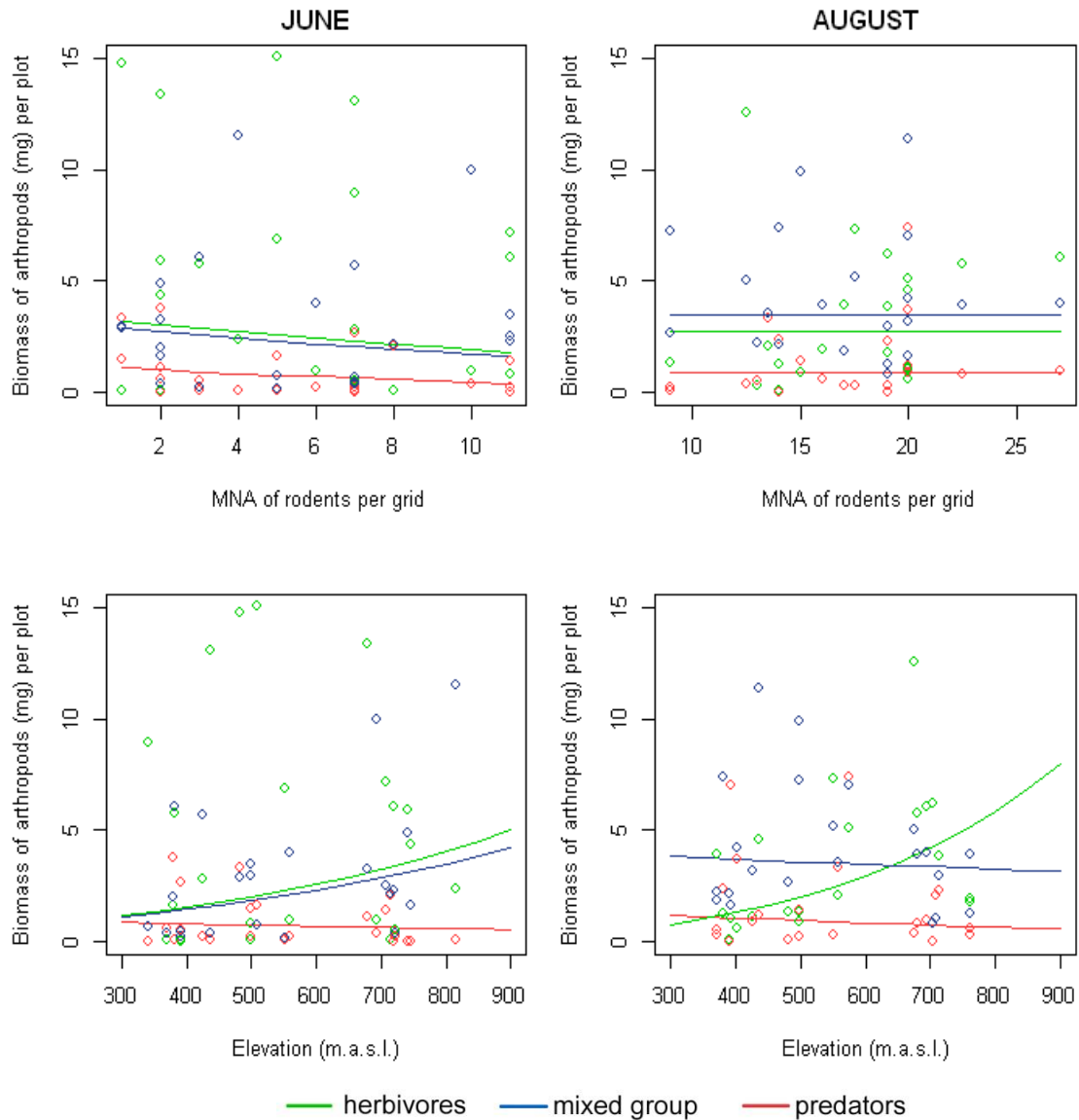
Figure 9: Responses of herbivores, mixed group and predators (measured as mg of biomass per plot) to changing rodent population density (predictor of main interest in the study) and to elevation (important in both months) in June and in August. Predictions in month **June** are made for *bilberry forest* vegetation type and activity during the *day* (part of the day). In **August**, predictions apply to *bilberry forest* and intermediate shade (*20 – 80 %*). To predict response for rodent density I used in addition mean elevation in both months. Average rodent population was used in June to predict response to elevation in June. Since there was no effect of rodents in August they were not used to calculate the response to elevation in August. Dots represent observations of different arthropod groups corresponding to mentioned environmental and habitat conditions. Notice that rodent densities for two months differ.

In August, the effect of *rodents* on biomass of arthropods was not included in the model with the lowest AIC (Table 11). The best model comprised *shade* and two interactions - *functional group*vegetation type* and *functional group*elevation* (Table 11). Marginal effect of the model was $r^2 = 0.45$, and conditional effect $r^2 = 0.48$.

Table 11: Model selection according to AIC (ΔAIC and AIC weight) in August, where as the response variable was used biomass of arthropods per sampling plot and functional group. Table contains 10 terminal models out of 40 tested models with degrees of freedom (df) and corresponding AIC values. Models are displayed in descending order, starting with the best model on top. Interactions between predictor variable and *functional group* are denoted by symbol (*) in model formula.

Model	df	AIC	ΔAIC	AIC weight
Shade, Vegetation*Func., Elevation*Func.	28	591.40	0	0.26
Shade, Rodents, Vegetation*Func., Elevation*Func.	29	591.51	0.10	0.24
Shade, Part of day, Rodents*Func., Vegetation*Func., Elevation*Func.	33	592.19	0.79	0.17
Shade, Solar rad., Vegetation*Func., Elevation*Func.	29	592.46	1.06	0.15
Part of day, Vegetation*Func., Elevation*Func.	28	594.03	2.62	0.07
Vegetation*Func., Elevation*Func.	26	594.83	3.42	0.05
Solar rad., Vegetation*Func., Elevation*Func.	27	595.96	4.55	0.03
Rodents, Vegetation*Func., Elevation*Func.	27	595.98	4.57	0.03
Shade*Func., Vegetation*Func., Elevation*Func.	32	599.13	7.72	0.005
Part.of.day*Func., Vegetation*Func., Elevation*Func.	32	600.24	8.84	0.003

There was interaction between *functional group* and *elevation* (Figure 9), just as in June (Table 9, 10). However, now the most significant was the increase in herbivores compared to other two groups (Table 12). The results also show that the arthropods varied in functional composition according to the vegetation type. *Swamp vegetation* and *rich clear-cut* had a higher biomass of herbivores compared to *pine forest with lichens*. There was no interaction between *functional group* and *vegetation types* in June, and three feeding guilds were spread equally (Table 9, 10). In August, shaded areas (> *80 %*) yielded higher biomass of arthropods than did more open areas with intermediate shade (*20 – 80 %*), whilst *shade* was not included in the model in June. On the other hand, I did not find any variation in activity of arthropods throughout the day (*part of the day*) in August, as I found in June (Table 11, 12).

Table 12: Summary table from the selected final model in August. The model explains variation in biomass of arthropods. The table displays log-transformed estimates with standard errors (SE), degrees of freedom (df), and t- and p-values for numerical predictors and for each factor level. The intercept includes the categories *pine forest with lichens* (vegetation type), *shade 20 – 80 %* (shade) and *mixed group* (functional group). The estimates of the other factor levels are relative to the intercept.

	Estimate	SE	df	t-value	p-value
Intercept	0.89878	0.38428	254	2.34	0.02
Pine forest (dwarf shrubs)	0.23369	0.33691	254	0.69	0.49
Bilberry forest	0.74692	0.23233	254	3.21	0.002
Ferns – shrubs forest	0.46086	0.26073	254	1.77	0.08
Swamp vegetation	0.38993	0.38413	254	1.02	0.31
Poor clear-cut	0.19085	0.28416	254	0.67	0.50
Rich clear-cut	0.43703	0.30449	254	1.44	0.15
Shade < 20 %	0.11703	0.10697	254	1.09	0.28
Shade > 80 %	0.35936	0.13513	254	2.66	0.008
Herbivores	-1.74979	0.43021	254	-4.07	< 0.001
Predators	-0.68433	0.43021	254	-1.59	0.11
Elevation	-0.00024	0.00062	254	-0.40	0.69
Pine (dwarf shrubs) : Herbivores	0.15619	0.47503	254	0.33	0.74
Bilberry : Herbivores	-0.15293	0.32262	254	-0.47	0.64
Ferns - shrubs : Herbivores	-0.49961	0.34730	254	-1.44	0.15
Swamp : Herbivores	1.40714	0.53615	254	2.62	0.009
Poor clear-cut : Herbivores	0.66836	0.39522	254	1.69	0.09
Rich clear-cut : Herbivores	1.26378	0.42221	254	2.99	0.003
Pine (dwarf shrubs) : Predators	0.37151	0.47503	254	0.78	0.43
Bilberry : Predators	-0.01872	0.32262	254	-0.06	0.95
Ferns - shrubs : Predators	0.25836	0.34730	254	0.74	0.46
Swamp : Predators	0.66019	0.53615	254	1.23	0.22
Poor clear-cut : Predators	0.11321	0.39522	254	0.29	0.77
Rich clear-cut : Predators	0.17132	0.42221	254	0.41	0.69
Herbivores : Elevation	0.00297	0.00070	254	4.24	< 0.001
Predators: Elevation	-0.00030	0.00070	254	-0.43	0.67

4. Discussion

4.1 Interactions with rodents

My data suggests a potential impact of rodents on the arthropods in the month of June, but not so in August. The orders Diptera and Collembola had the strongest negative relationship between abundance and rodent density in June. The orders Hemiptera, Thysanoptera and Opiliones were slightly positively related to rodent density. All functional groups of arthropods (herbivores, predators and mixed group) showed a decline in biomass with increasing rodent density in June.

This result contradicts my expectancy of a negative effect of rodents on biomass of herbivorous arthropods in the period of high rodent density (August) when potentially many plants have accumulated high level of secondary metabolites as induced defence caused by rodent grazing. This finding can be explained by the plant-age hypothesis considering plant ontogeny (Bryant *et al.* 1992). The hypothesis assumes high level of defensive traits in intensively growing tissues of seedlings and juvenile stages as damage of these tissues may have serious consequences for plant fitness. My results are in accordance with this hypothesis and with findings of Barton and Koricheva (2010), who attempted to identify a pattern in plant defence in relation to plant ontogeny by using meta-analysis. They described a steep increase in constitutive defence during seedling and juvenile stages, higher level of induced defence in juveniles compared to mature plants, and decrease in defence through mature stages. The process supports the occurrence of indirect interactions between rodents and arthropods early in the season. In comparison with induced defence which is activated by herbivore damage, constitutive defence incorporates toxins permanently present in a plant, presumed to prevail in those tissues which are under high risk of herbivore attack (Wittstock & Gershenzon 2002). I did not mention constitutive defence previously as it is regulated by the plant itself and not by herbivores, but I assume it might also play a role in my study system. In the study of Barton and Koricheva (2010) small mammals have been found to favour mature plants over juveniles. Although most rodent species in boreal forest are considered to be herbivorous, diet analyses revealed certain proportion of insects in their diet (Hansson 1970; Stenseth, Hansson & Myllymäki 1977; Hansson 1979; Bostrom & Hansson 1981). I assume that in times of well-defended plants, larvae and imagines of

arthropods might serve as an important alternative food source for rodents, indicating a direct interaction of rodents on arthropods.

The different responses of the arthropod orders to rodents might be related to the vegetation type creating differently functioning systems in a boreal forest limited by nutrients (Bryant, Chapin III & Klein 1983). Hemiptera and Thysanoptera which were positively related to rodent densities occurred mainly in clear-cuts which had high proportion of graminoids, while Diptera and Collembola which were negatively related to rodents, were associated with ferns-shrubs forest. According to Bryant, Chapin III and Klein (1983) graminoids accumulate carbon in below ground reserves and respond to herbivory by compensatory growth. This would mean there was additional food resource available for the arthropods. On the contrary, slowly growing evergreen and woody plants are well defended as the replacement of lost tissues due to herbivory is costly. Populations of arthropods in such a system might suffer from both, direct and indirect effects of rodents. Lastly Opiliones which also showed a weak positive response to rodents were associated with bilberry forest. The order represents the predatory guild and therefore the response corresponds with my hypothesis, stating that herbivorous arthropods become easy prey due to altered feeding behaviour activated by decreased food availability.

Based on the above mentioned studies, the outcome of the analyses regarding rodents might be either result of direct interaction (predation of rodents on arthropods), plant - mediated indirect interaction (induced defence, compensatory growth, or other plant responses triggered by rodents), or a combination of both interactions.

In general, herbivory is one of the factors perceived to impose stress on the plants (Speight, Hunter & Watt 2008, p.79). Two hypotheses are commonly discussed in context of insect herbivore performance. The plant stress hypothesis, sometimes also called increased vulnerability hypothesis (Mysterud *et al.* 2005), predicts that insect herbivores will prefer plants under stress and will benefit from increased grazing intensity (White 1969), whereas the plant vigor hypothesis, similar to increased defence hypothesis (Mysterud *et al.* 2005), suggests that herbivores prefer to feed on plants and plant modules which grow vigorously, in terms of size and growth rate (Price 1991). My study does not support any of these very general hypotheses, but showed the effect of grazing intensity is subordinated to vegetation type and plant ontogenetic stage, possibly in combination with behaviour of the arthropods.

At present more complex studies investigating indirect interactions between mammalian herbivore and arthropods / insect community are on the rise. However, existing studies mostly consider large herbivores due to their prominent effects on the environment

and plant community, e.g., moose (Danell & Huss-Danell 1985; Mathisen 2011), deer (Allombert, Stockton & Martin 2005), reindeer (Suominen *et al.* 2003) or beaver (Martinsen, Driebe & Whitham 1998), and sometimes focus only on one specific group of invertebrates or few particular species (Neuvonen & Danell 1987; Strauss 1991a). I did not find any study investigating indirect effects of rodents on the arthropod community in the boreal forest zone. Differences in methodological approaches, ecosystem productivity and specific arthropod adaptations make comparisons across a wide range of ecosystems difficult. The effects of vertebrate herbivores on arthropods found in other studies are of all kinds - positive, indifferent or negative.

Allombert, Stockton and Martin (2005) found a significant decline in abundance of distinct insect orders (all except Coleoptera) and overall insect abundance with increasing length of deer browsing. Similar to my study, the habitat type was important type in shaping the relationship between browsing and arthropod abundance. They reported the herbivore guild, in particular orders Heteroptera and Homoptera (in this study corresponding to Hemiptera), to be more negatively affected by browsing than predators and parasites. However, the study took place on islands and may therefore be difficult to compare with my study due to isolation, restricted colonization and different evolutionary formation of the species and interactions compared to mainland (Case & Cody 1987). Danell and Huss-Danell (1985) found a positive effect of moose winter browsing on leaf area and quality, reflected in higher occurrence of herbivorous insects and ants. They concluded that the outcome depended on the period when browsing occurred (browsing during winter versus during growing season). Varying moose density in the study of Mathisen (2011) affected richness of flower-visiting insects (Hymenoptera, Diptera), but not the overall abundance. Usually studies focus on arthropod species richness and abundance to test the intermediate disturbance hypothesis (Fox & Connel 1979), while most of them also track the response of plants to herbivory (Bailey & Whitham 2002; Suominen *et al.* 2003). However, I did not investigate species richness and diversity, and higher richness in arthropods is not inevitably correlated with abundance (Mathisen 2011).

4.2 Habitat and environmental predictors

Responses of arthropod abundance and biomass to the other predictors, which were used to explain variation due to changing environmental and habitat conditions, differed. Some of these effects are difficult to explain as they may be related to the biology of

arthropods which is still fairly unknown. The results showed a relatively high proportion of unexplained variance. It means there were either other factors driving the arthropod populations which I did not account for, or it may be a sign of fluctuations in arthropod populations which make their communities to a great extent unpredictable (Strong, Lawton & Southwood 1984). Alternatively it might be due to sampling errors. The environmental predictors I used explained more variance in arthropods, both in biomass and abundance, in August than in June.

None of the analyses indicated variation in arthropods due to **solar radiation**. I suspect this does not mean that solar radiation is unimportant, but rather its effect is masked by other interrelated predictors – specifically by vegetation type, part of the day and shade. For example, dark, humid forest with ferns and shrubs will most likely grow on a surface facing north. Similarly time of day (morning, day, evening) might track changes in radiant energy due to the motion of the sun. Shade from canopy cover directly determines how much sunlight is received by the ground. I assume that these predictors simply outbalanced the effect of solar radiation as they include additional information.

The analyses clearly confirmed importance of the **vegetation type** for the arthropod communities. Differences among vegetation types in plant biomass and plant diversity were reflected in yield of the arthropod biomass. The lowest biomass of the arthropods was sampled in pine forest with lichens, which is characterized by poor plant species diversity, low plant biomass and monotony. On the other hand the highest biomass of the arthropods was sampled in rich clear-cuts where the plant community is rich and diverse. This is in accordance with Price (1992) who assumes dependence of arthropod herbivores followed by their natural enemies on carrying capacity determined by available plant biomass, depending on stage of succession and specialization of arthropods.

Abundance of distinct orders varied according to the vegetation type. The order Hemiptera was the most abundant in rich clear-cuts and in habitats with swamp vegetation, together with Trichoptera and Thysanoptera. Collembola and Diptera were abundant above the average in ferns – shrubs forest. In August most orders with the exception of Hemiptera and Thysanoptera had the highest abundances in bilberry forest. These associations are predictable though. Rich clear-cuts receiving a lot of sunlight and being diverse in plant composition presumably provided herbivorous arthropods (Hemiptera) with sufficient amount of food and with suitable conditions for the development of thermophilous species. As the larval stage of Trichoptera is aquatic, they usually occur close to water, what would explain their association with swamp vegetation in this study (Chinery 2007, p. 183).

However, I highlight the low sample size for swamp vegetation (4). Although Diptera is a very diverse order, dependence of some groups on humid conditions has been documented (Dahl 1969). Similarly Collembola typically lives in humid habitats (Southwood 1973).

The effect of **elevation** was also important for the biomass of arthropods. The functional groups did not correlate uniformly though, but their responses varied. During both months, herbivore biomass increased and predator abundance decreased with increasing elevation. Biomass of mixed group increased with elevation in June and decreased in August. Interestingly, the finding is in partial agreement with Hodkinson (2005) who investigated arthropod communities along an altitudinal gradient and disapproved the idea of distribution around the optimum. With increasing elevation, the communities undergo various changes in environmental conditions (e.g., temperature lapse rate, decrease in oxygen, wind speed) and changes in host plants (e.g., phenology, morphology, chemicals, responses to stress). He gathered evidence for a general decrease of parasitoids and predators with increasing altitude caused by lower searching efficiency in temperatures below optimum, although with weaker evidence for predators. Response of herbivores is given by tritrophic interactions including host plants and predators / parasitoids.

Shade affected abundance of different arthropod orders in the month of June, and biomass of the functional groups in the month of August. Naturally, the orders associated with clear-cuts (Hemiptera, Thysanoptera, Trichoptera) were associated with unshaded areas (*< 20 %*). The rest of the orders occurred in above average abundances in habitats with intermediate shade (*20 – 80 %*). In August shady habitats (*> 80 %*) yielded higher biomass of arthropods than places with more sun shining through the canopy (*20 – 80 % shade*).

In June functional groups showed variation in biomass according to **part of the day**. Groups of herbivores and predators were less active in the evening when mixed group predominated. In the ordination analysis, part of the day explained some variance in August. Particularly important was the category morning, which was however represented by only few observations (5). Collembola and Araneae were more active in the morning, while Hemiptera and Coleoptera were less active.

Both findings, higher arthropod biomass in shaded areas and variation in arthropods catch during the day, might be related to time-specific moisture and temperature levels of a habitat and to the biology of arthropods (e.g., regulation of body water content). There are studies documenting higher biomass in moist habitats (Remmert 1981), as well as studies documenting flight activity (e.g., swarming) varying with changes in temperature and humidity (Dahl 1969).

4.3 Study design

The original plan of the BEcoDyn project was to manipulate rodent density in the six localities (localities with high rodent densities provided by supplementary feeding, localities with reduced density using trapping, and control localities without manipulation). However, the project failed to reach these purposed states. As an alternative solution, I used observations from trapping grids instead, representing natural variation in rodent density. Study design in this performance however showed up as suboptimal for observing the indirect interactions carried from rodents on the arthropods due to several shortcomings.

The most serious drawback was unequal distance among rodent trapping grids and arthropod sampling plots, causing a loose link between rodents and arthropods. The ideal solution would be to monitor rodent density specifically in the plots where I sampled arthropods, or to sample arthropods only in locations of the trapping grids.

Regarding the categorical predictor variables, *vegetation type* and *part of the day* were unbalanced in the data. Categories of these variables were represented unevenly in the samples. A solution might be to collect samples at a given time of the day, or to apply numerical measurements of environmental conditions like temperature, humidity and barometric pressure, which profoundly influence activity of arthropods (White 1973). Avoiding categorization and rather using accurate numerical measurements would bring more precision into the data and would facilitate the analyses. The same principle applies to vegetation type which is an essential determinant of habitat conditions for arthropods, but quite coarsely registered in this study.

Using sweeping to sample the arthropods for quantitative assessment may have consequences for the outcome of the study as the technique is subjective and prone to error. In addition, arthropod data used for biomass analysis of functional groups could be utilized more efficiently if the arthropods would be identified to family instead of the order. That would allow reducing the mixed group and possibly including more feeding guilds.

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Appendix A

Description of vegetation types used in classification of sampling plots:

1. **Lichen Pine forest**

   Open, very dry forest on poor, barren soils, dominated by Scots pine (*Pinus sylvestris*), possibly with a mixture of downy birch (*Betula pubescens*). Dwarf shrubs dries quickly and is developed only sparsely. It is characterized by crowberry (*Empetrum nigrum*), lingonberry (*Vaccinium vitis-idaea*), bilberry (*Vaccinium myrtillus*), and heather (*Calluna vulgaris*). In addition, drought tolerant grasses make up the dwarf shrubs - eg. wavy hairgrass (*Avenella flexuosa*), sheep fescue (*Festuca ovina*). Cup lichens (*Cladonia* sp.) creates continuous mats over a large areas, typically *C. stellaris*, *C. arbuscula*, *C. rangiferina*. Moss cover is generally very low, but some acrocarp species may be present.

   A: poorly developed understory, mostly *Cladonia* sp. only
   B: dwarf shrubs species are more abundant

2. **Bilberry forest**

   Relatively old, highly productive Norway spruce (*Picea abies*) or mixed Norway spruce/ Scots pine forest with dominance of bilberry in the dwarf shrubs. Grasses and some herbs may be present - eg. wavy hairgrass, cowwheat (*Melampyrum* spp.), May lily (*Maianthemum bifolium*), arctic starflower (*Trientalis europaea*). The two pleurocarp moss species which can grow in all specified vegetation types - *Hylocomium splendens* and *Pleurozium schreberi*, are the most abundant in this forest type.

3. **Ferns - shrubs forest**

   Coniferous forest on mesic to moist soils with a dense tree layer. Characteristic are small fern species, oak fern (*Gymnocarpium dryopteris*) and long beech fern (*Phegopteris connectilis*). Bilberry occurs in substantially smaller proportion compared to category 2) Bilberry forest. In more rich formations may be present herbs and grasses mentioned in previous category. Wood sorrel (*Oxalis acetosella*) is a characteristic herb species. Pleurocarp mosses typical for humid sites create field layer – *Brachythecium* sp., *Hylocomiastrum umbratum*, *Mnium* sp.

4. **Swamp vegetation**

Swamp vegetation in this study merges all formations with typical moisture demanding species. Peat moss (*Sphagnum* spp.) is particularly typical species building up well developed field layer. From other moss species are characteristic eg. *Campilium stellatum* and *Scorpidium revolvens*. Tussocks of sedge (*Carex* sp.) and rushes (*Juncus* sp.) indicate waterlogging habitat. Grasses like purple moor-grass (*Molinia caerulea*) and cottongrass (*Eriophorum* sp.), as well as some herbs may occur, eg. cloudberry (*Rubus chamaemorus*). Crowberry and heather in bottom layer are developed only sparsely.

5. **Forest with open tree layer after logging (clear cut)**

Norway spruce and Scots pine forest with open tree layer after logging, with a mixture of deciduous tree species - downy birch, European aspen (*Populus tremula*). Heliophilous species are highly abundant and in favour due to the profusion of light reaching the field layer.

A: *poor, dry type*

Typical dwarf shrubs species are heather, crowberry and lingonberry, accompanied with grasses like wavy hairgrass, nard grass (*Nardus stricta*) and purple moor grass (*Molinia caerulea*). Lichens (mainly *Cladonia* sp.) and drought tolerant moss species are part of the field layer - *Dicranum* sp.: *D. drummondii*, *D. fuscescens*, *D. polysetum*, *D. spurium*; *Polytrichum juniperinum*, *Racomitrium lanuginosum*.

B: *rich type*

Heliophilous and nitrogen demanding / tolerating species constitute a substantial amount of the vegetation. Compared to the dry type, species richness is much higher. Typical is occurrence of multiple grass species (eg. hairy wood-rush (*Luzula pilosa*), common bent grass (*Agrostis capillaries*), wavy hairgrass, finger sedge (*Carex digitata*), purple reedgrass (*Calamagrostis arundinacea*). Other characteristic species are fireweed (*Chamerion angustifolium*), May lily, common nettle (*Urtica dioica*), ragworts / groundsels (*Senecio* spp.), bracken fern (*Pteridium aquilinum*), raspberry (*Rubus idaeus*) and red-berried elder (*Sambucus racemosa*).