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Change in arthropod communities following a mass death incident of reindeer at Hardangervidda

Heidi Mørkhagen Granum
Master of Science in Ecology
Faculty of Environmental Sciences and Natural Resource Management

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1. Introduction

Decomposition of dead material is a vital part of ecology and an important process for sustaining biodiversity in an ecosystem, as dead organic material or detritus is the basis of all food webs. A fundamental truth is that everything dies, and without the processes of decomposition and decay the world would quickly become buried in dead plants and animals while new growth would decline due to lack of nutrients. (Featherstone). One of the most important features of decomposition is that it allows nutrient recycling, by breaking down tissue and macro-elements into nutrients such as carbon, nitrogen and phosphorus, which can be utilized again by a variety of organisms, instead of being locked up in dead or inorganic forms. Detritus is an important resource for all organisms, and it connects all organisms to the cycling of energy and nutrients (Barton et al. 2013).

It is estimated that approximately 99% of the organic matter that undergoes decomposition is plant-derived, at least for terrestrial ecosystems (Carter et al. 2007). Research on decomposition of dead animals (carrion) has therefore received less focus during the last decades, especially in Europe. In addition to the low amount of biomass as compared to plants, experiments with carcasses are also strongly regulated (Gu et al. 2014). This could be because it is sometimes hard to conduct studies, or simply because humans typically perceive carcasses as repulsive. However, cadaveric resources is nutrient-rich compared to plant litter, and may therefore play a major part in sustaining species that utilize carcasses as a resource. These species range from mammals, birds, and arthropods, to fungi, soil-living microbes and vegetation.

Here, I define cadavers or carcasses (Figure 1) as dead animals, of whom their bodies can be partly consumed by scavengers and/or predators, and/or undergo decomposition. Carcasses often become hotspots for a myriad of species, and they typically represent an “island”, with the surrounding nature acting as the ocean (Cadaver Decomposition Islands, CDIs) (Carter et al. 2007). The island term refers both to the dead vegetation under and around the carcass due to abrupt changes in soil biogeochemistry and vegetation, and the fact that the cadaver represents an “island” of both nutrition and disturbance in an “ocean” of plant material. The cadaver generates different conditions on a small scale that allow many species form several

kingdoms to thrive during secondary succession (Carter et al. 2007). Small scale effects include the changes we can observe within the local ecological communities when a carcass suddenly becomes available as a food source. On a small scale, sessile functional groups or groups with low mobility, such as mites, vegetation and microorganisms are typically more affected by the presence of a carcass, as they cannot 'evade' the local disturbance.

Figure 1: Reindeer carcasses at the Hardangervidda plateau, Norway, June 2018. The carcasses originate from a mass die-off due to a lightning strike on 26 August 2016 and killed 323 animals. Photo by Heidi Mørkhagen Granum.

The resources provided by carcasses is being competed for by a wide array of animals, insects, and microbes (Carter et al. 2007). In some insect rich areas, insects can consume a carcass before even one singe vertebrate scavenger has utilized it (DeVault et al. 2004), removing up to 90% of tissue from small vertebrate carcasses in only a few days (Olea 2019). Large carcasses are often associated with a higher number of species (Gu et al. 2014), as they provide more organic material and the possibility of more niches. They also contribute to a larger amount of nutrients being deposited into the food webs.

Arthropods have an extraordinary contribution to carcass decomposition. They are mobile, and thus able to actively search for carcasses. In a study done by Carvalho et al. 2000, the authors found that the insects were the most important decomposition agents of pig (*Sus scrofa*) carcasses, and other studies have found larger species richness of insects on carcasses compared to a control area without carcasses (Melis et al. 2004, Sikes 1994). Many of the species found near or on carcasses are specifically adapted to consume carrion or any kind of decaying material (Melis et al. 2004). Insects are also the most species-rich and abundant organisms found on dead animals other than microbes (Braack 1987). As a vital part of the food web, also in carrion communities, insects contribute to the consumption, and recycling and dispersion of carrion derived nutrients (Parmenter and MacMahon 2009). Without arthropods, it is likely that the decomposition process will be delayed (Pechal et al. 2014).

Typically, the species composition associated with a carcass changes gradually over time, along with decomposition, and insect abundance generally declines over time (Anderson 2007). A carcass goes through several stages of decomposition, from fresh to finally dry/remains (Payne 1965, see Appendix 1, Table S1). Blowflies (*Calliphoridae*) and flesh flies (*Sacrophagidae*) seems to be the most important group that contribute to mass loss in a carcass at early stages of decomposition (Carvalho et al. 2000, Lashley et al. 2018), which Linnaeus 1767 theatrically expressed: “three flies could consume a horse cadaver as rapidly as a lion”. However, a large number of beetles (*Coleoptera*), such as carrion beetles (*Silphidae*), ground beetles (*Carabidae*), rove beetles (*Staphylinidae*), and sap beetles (*Nitidulidae*) are also found on and near carcasses at various decomposition stages (Melis et al. 2004). *Coleoptera* species are often abundant on and near carcasses, and some species can act as indicator species for an area where carcasses are present.

Diptera and *Coleoptera* species are often attracted to specific stages of carcass decomposition, which can make them important in determining time since death in human cadavers (Carvalho et al. 2000). This feature is often used in forensic studies. Not only carrion species are affected by a carcass. A decomposing animal may induce ecological effects to promote increased diversity among *Hemiptera*, *Hypenoptera*, *Lepidoptera* and various *Diptera* species (Gu et al. 2014, see Appendix 1, Table S2).

A carcass is not only a source of food for scavengers or breeding ground for a number of insects. A large carcass (e.g. many ungulate species) also allows for considerable amount of nutrients to enter the soil, because the carcasses are too big to be entirely consumed or carried away by scavengers (Carter et al. 2007). Studies have shown that a number of nutrients associated with decomposition such as phosphorous, potassium, calcium and ammonium are present in high concentrations up to five years after the decomposition process is over (Towne 2000, Vass et al. 1992). The sudden availability of nutrients concentrated in the carcass mediates the local conditions, which typically results in a local change of species interactions with the carcass constituting the center. For example, scavenger insects may affect other trophic levels such nematodes in the soil, or birds feeding on the insects. Pioneer vegetation that emerges after the decaying process is over can further interact with insects and herbivores. Thus, we can observe a cascade of events caused by decomposition, both enriching and disturbing the surrounding ecosystem (Lashley et al. 2018).

Scavengers and insects are able to disperse nutrients over large distances during the decomposition process (Barton et al. 2013), making a carcass an important source of nutrients on a large scale. The large scale effects imply the changes that can be observed on the landscape scale, such as when scavengers localize a carcass from further away and are attracted to the area. Functional groups with high mobility can induce these wider effects, given that they often actively search for prey species and can travel long distances to get to a carcass. Carcasses may also contribute to plant biodiversity on the landscape scale, and scavengers can disperse plant seed picked up across the landscape towards carcasses, through endozoochory (Steyaert et al. 2018). The separation between small scale and large scale effects is appropriate for distinguishing which responses to expect from different taxonomic groups in studies that involves carcasses.

Most carcasses are found in small numbers, often alone, and mass-die offs with spatially clustered carcasses are considered rare. In 2016, researchers placed 3 tons of dead pigs out in the open in the forests of Mississippi to observe the decomposition process (Wilcox 2017) at such a mass die off. This study revealed interesting interactions and potential large scale effects, and the role of mass-death of animals in ecosystems have consequently received increased attention in the scientific literature, provided their potential disproportional role in ecosystem functioning. (Lashley et al. 2018, Steyaert et al. 2018, Subalusky et al. 2017).

Due to a lightning strike, an entire herd of wild tundra reindeer (N = 323, *Rangifer tarandus*) was killed in Hardangervidda, Norway, on 26 August 2016. This alpine area is now being used as a field laboratory by researchers following their decomposition process and its ecological impacts (Steyaert et al. 2018). As insects and other arthropods play a vital part of breaking down and consuming dead material, the main goal of this thesis is to assess how such a mass die-off affects the insect community in this alpine tundra ecosystem. Considering a time lag of about two years between the actual event and the fieldwork conducted for this thesis, the results will show if carcasses can continue to affect insect communities even two years after death. I will be able to determine which species are associated with carcass decomposition even two years after the incident, and also look for differences in arthropod communities within he carcass site (small scale) and between the carcass site and a control site (large scale).

My thesis represents a novel study, as mass die-offs are scarce in nature, and are poorly investigated with respect to many scientific disciplines. Most studies conducted on arthropod activity and communities relate to single carcasses that have been physically placed by researchers (mostly in forensic studies). Furthermore, Barton et al. 2013 found a strong bias towards conducting carrion arthropod studies in forested areas, and suggest a need for studies in a wider environmental range. Filling the gap in our knowledge on the importance of carrion for arthropod species in different environments can also be relevant to the conservation of biodiversity, by changing the way we treat carcasses and dead animal material.

Hypothesis and predictions

The main hypothesis of this thesis is that reindeer carcasses structure the community of arthropods in the alpine tundra, even two years after a mass death-incident, both on a small scale and on a large scale. Hence, I predict that:

i) On a large scale, an area where carcasses are present will have a higher number and diversity of arthropods compared to a similar area without carcasses

ii) Where the carcasses are present, the total abundance of predators and detritivores will be higher, while the abundance of herbivores will be lower compared to a similar area without carcasses

iii) On a small scale, within the area where carcasses are present, the number of predators and detritivores will increase with a decreasing distance to the nearest carcass

iiii) There will be more *Coleoptera* indicator species in an area where carcasses are present, and a higher proportion will be predatory compared to a similar area with no carcasses

2. Materials and methods

2.1. Study area

The study area is located in Hardangervidda, Norway, at 1220 m a.s.l. (Figure 2). Hardangervidda is Europe's largest high-mountain plateau and encompasses about 8,600 km^2. The inner core of Hardangervidda is one of the largest national parks in Europe. It inhabits many species of bird and several mammals, including the wild tundra reindeer (Hardangervidda.com 2018). About one quarter of all remaining wild tundra reindeer lives here. The alpine tundra ecosystem has a relatively species poor community which is dominated by dwarf birch (*Betula nana*), ericaceous shrubs (e.g. crowberry (*Empetrum nigrum)),* graminoids, mosses and lichens (Steyaert et al. 2018).

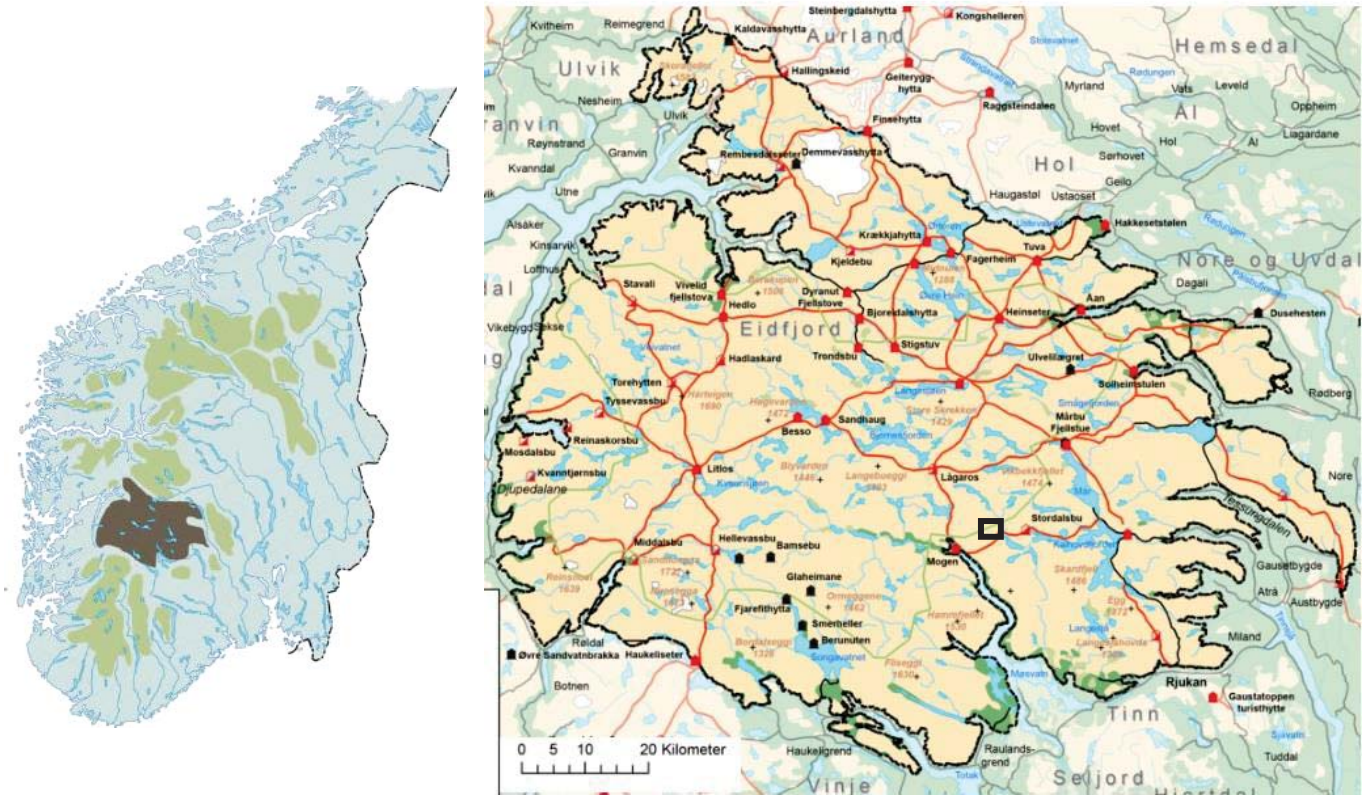

Figure 2: Overview map of Hardangervidda (right panel) and its location within Norway (left panel, dark green). The black square represent the area where the carcasses are located. Source: http://www.villrein.no/hardangervidda-2/.

On 26th of August 2016, lightning killed 323 reindeer near the Vesle Saura lake in the southern part of Hardangervidda. The carcasses are distributed over an area of 240 x 100 m, with the highest concentration comprising no more than about 50 x 50 m (Figure 3). The REINCAR project established 75 permanent monitoring plots (e.g. soil biogeochemistry, vegetation) in a semi-regular grid, covering the entire area (Steyaert et al. 2018).

Figure 3: Survey plots (black dots) and carcass distribution (grey dots) at the study site in Hardangervidda. Circles highlights the survey plots used for trapping. Figure adapted from Steyaert et al. (2018).

To assess the impact of carcasses on the arthropod communities, both on a small and a large scale, I established a control area without carcasses. This is one of the most basic ways assess the impact of any treatment on any object, and especially relevant when differentiating between carrion-associated and non-carrion associated species (Melis et al. 2004). The control area is located approximately 500 m away from the carcass site, with a similar composition of plant life and abiotic factors (both are eastern hillsides at approximately the same altitude). Of the 75 survey plots in the carcass area, 30 were used for trapping arthropods. These 30 plots, highlighted in Figure 3, were chosen based on their placement in the already existing grid, starting further away from the cluster of carcasses and moving towards the high densities, giving the opportunity to check for differences in arthropod composition in relation to carcass proximity. I spaced a similar grid of 30 plots to be used for trapping in the control area.

2.2 Data collection

I used two trapping periods from June to August, 2018:

- From 12/13 June – 17/18 July
- From 17/18 July – 3/5 August

The initial plan for processing the insect material at the lab was to assess all traps for both periods. However, only the contents from the first trapping period was assessed due to the long time needed for sorting and identification in the lab.

On 12 and 13 June 2018, I installed 30 pitfall traps (Figure 4) in both the carcass area and the control area, a total of 60 traps, using the plots in the grids. Pitfall traps have proven to be effective for capturing arthropods and yield reliable data (Gu et al. 2014, Melis et al. 2004, Sikes 1994). The traps had a diameter of 9 cm and were and 7 cm deep. Plexi glass square roofs covering the traps were attached to the ground with wire, to protect the trap contents from rainfall or evaporation. I added 125 ml of 50% propylene glycol mixture to each of the traps for its preservative and properties (Thomas 2008). I also added a small amount of dishwashing soap to break the surface tension of the mixture in the traps, allowing arthropods to easily sink to the bottom of the traps. All traps and lids were marked with permanent marker and their GPS positions were recorded.

I distributed 15 sticky traps (Figure 5) in both areas, with one sticky trap for every second pitfall trap, totaling 30 sticky traps. Passive sticky traps have proven effective to sample arriving, flying insects (Cruise et al. 2018). The traps consisted of white plastic lids (15 cm diameter), covered with a thin layer of Tanglefoot^{TM} applied at the inner side of the trap. The sticky traps were attached to bamboo poles, 50-100 cm above the ground, and marked with permanent marker. A summary of the total number of traps in both sites can be found in Appendix 1, Table S3.

Figure 4: Setup of the pitfall traps. The number C23 indicates that this is trap number 23 in the control area. Photos by Heidi Mørkhagen Granum.

I collected pitfall trap content and the sticky traps for the first time on the 17th and 18th of July 2018. To collect the pitfall traps, the content in the traps was poured over mesh tissue (Figure 6), filtering out the trap content from the propylene glycol. The used propylene glycol was carried back and disposed in the lab to avoid contamination of the study site. The sticky traps were removed from the bamboo poles and replaced. All traps were reinstalled after the initial collection. I repeated the collection procedures on 3-5th of August 2018, after which all traps were also removed.

Figure 5: A sticky trap in the carcass area after 5 weeks. Photo by Tonje Mørkhagen.

Figure 6: Mesh tissue with content from a pitfall trap. Photo by Tonje Mørkhagen.

I assessed trap content in the lab, and divided the arthropods community into functional groups. The main functional groups were predators, herbivores, detritivores, *Diptera* and mites. All taxonomical groups and functional groups are listed in Appendix 1, Table S4. The groups included in the functional group "Omnivores/others" are not included in further statistical analyses as they are not predicted to be significantly affected by the presence/absence of carcasses because their feeding patterns are so widely ranged. In addition, the *Coleoptera* species from all the assessed pitfall traps were determined to species level by an expert (Sindre Ligaard), to be able to run the indicator species function. This will show how many species of *Coleoptera* are especially associated with either the carcass site or the control site, and also which species are associated with either of the two sites. A high indicator value implies that a species is strongly associated with one site.

The sticky traps were divided into three categories based on the level of coverage (low, medium or high). This categorization were done by two volunteers that were unaware to which of the two sites (carcass vs. control) the traps belonged. All pitfall trap content is stored in ethanol, and the sticky traps are stored in a freezer.

2.3 Statistical analyses

The dataset was processed in excel for Windows, and the statistical analyses were conducted in R. Generalized linear models (GLMs) were run with a negative binomial fit to determine how habitat (carcass vs. control) affected the total number of individuals in general, and for the five main groups described above. All these models were ran as separate models, with the only explanatory variable being site (carcass/control). Density distribution plots were made for both the total number of individuals in both sites, and for each of the five main groups as visual support for the GLM results.

I composed an ordination plot to determine whether some taxonomic groups were more associated with either carcass or control plots, and to visualize whether some groups were likely to appear in close proximity to each other (e.g. same pitfall trap). This was done by running Non-metric Multidimensional Scaling (NMDS) ("vegan" package needed), and doing a permutation test to determine how well the two sites were separated in terms of structure

and composition on of the insect community. The group omnivores/others were included in this ordination plot. By doing this, I could visualize relationships between species composition patterns in relation to the two sites.

I calculated the Shannon's diversity index on the plot level for all 60 pitfall traps, and ran GLM (family = Gaussian) to determine if the diversity index differed between the two sites. I also ran GLM with the diversity index as a response variable to assess the effect of distance to the nearest carcass on the Shannon's diversity index (for the plots at the carcass site only). I used the number of individuals as a response variable to assess the importance of distance to nearest carcass on the total number of individuals, and for each of the five main groups in the carcass site only.

I tested how site type affected the total coverage of insects on the sticky traps, by running Fisher's exact test for count data. I ran the indicator species function on the separate *Coleoptera*-data to see if some species were particularly associated with carcass or control plots.

3. Results

The raw data for the analyses done here is the total number of arthropods captured in the pitfall traps, and also the total number in the different functional groups (Table 2).

3.1. Large scale effects

3.1.1. Abundance

The mean number of arthropods per pitfall trap was significantly higher (more than double) at the carcass site (600) compared to the control site (291) (Figure 7, Table 1. Estimate: -0.724, std. error:0.101, p-value: < 0.001).

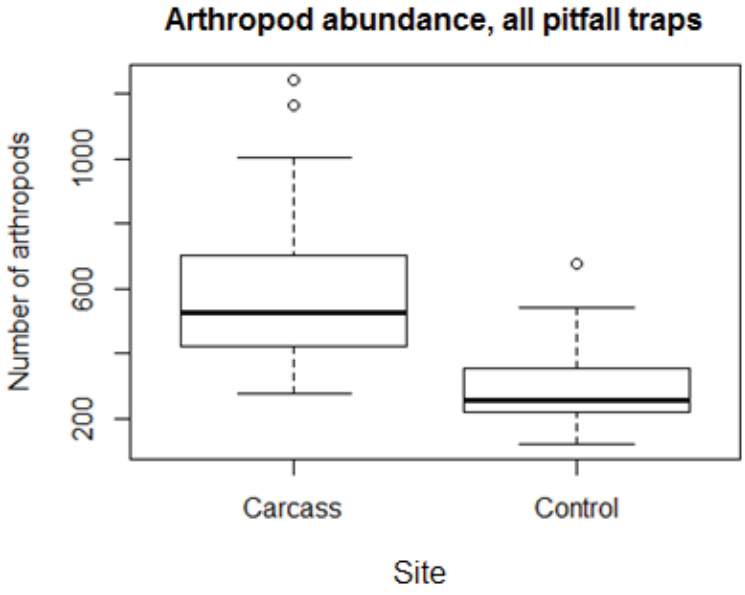

Figure 7: Boxplot of the number of individuals in the control site compared to the carcass site. Whiskers represent the 95 % confidence interval, black line represent the median, while the circles outside represents outliers.

Table 1: The total number of individuals captured in the pitfall traps in Hardangervidda 2018, and the total number for each functional group for both the carcass site and the control site. Not included are the group omnivores/others.

	Carcass site	*Control site*	*Total*
Number of individuals (omnivores included)	18 014	8 729	**26 743**
Predators, dominated by spiders, rove beetles and ground beetles	4 000	1 921	**5 921**
Herbivores, dominated by sapfeeders	262	306	**568**
Detritivores, dominated by carrion beetles	112	88	**200**
Diptera*, dominated by fungus gnats and flies (blowflies excluded, as they are included in detritivores)*	9 229	2 905	**12 134**
Mites, dominated by herbivore mites	1 023	2 172	**3 195**

There was a significantly higher abundance of predators and *Diptera* in the carcass site compared to the control site (Figure 8, Table 2). The mean number of predators per pitfall trap was more than double (133) in the carcass site, compared to the control site (64). The mean number of *Diptera* was more than three times as high in the carcass site (308) compared to the control site (97). The opposite was true for mites, which showed a significantly higher abundance in the control site. Here, the mean number was halved (34) in the carcass site, when compared to the control site (72). The abundance of herbivores and detritivores did not differ significantly between the sites (Figure 8, Table 2). Density distribution plots give an overview of the distribution of the arthropod data for further visualization. The density plot for the total number of individuals in both sites (Figure 9) clearly shows that a higher number of traps contains more than 500 individuals in the carcass site (black line in Figure 9) compared to the control site (grey line in Figure 9), and the five main groups appear as mentioned above (Figure 10).

Table 2: Generalized linear models were run in R with a negative binomial fit. The response is the total number of arthropods predicted by site for all pitfall traps (N=60). A negative estimate indicates the lower total number in the control site. Significant values are highlighted in bold for habitat type on the five main groups in each site.

	Estimate	*Std. Error*	*P-value*
Predators	-0.733	0.092	**< 0.001**
Herbivores	0.155	0.164	0.345
Detritivores	-0.241	0.259	0.352
Diptera	-1.156	0.173	**< 0.001**
Mites	0.753	0.139	**< 0.001**

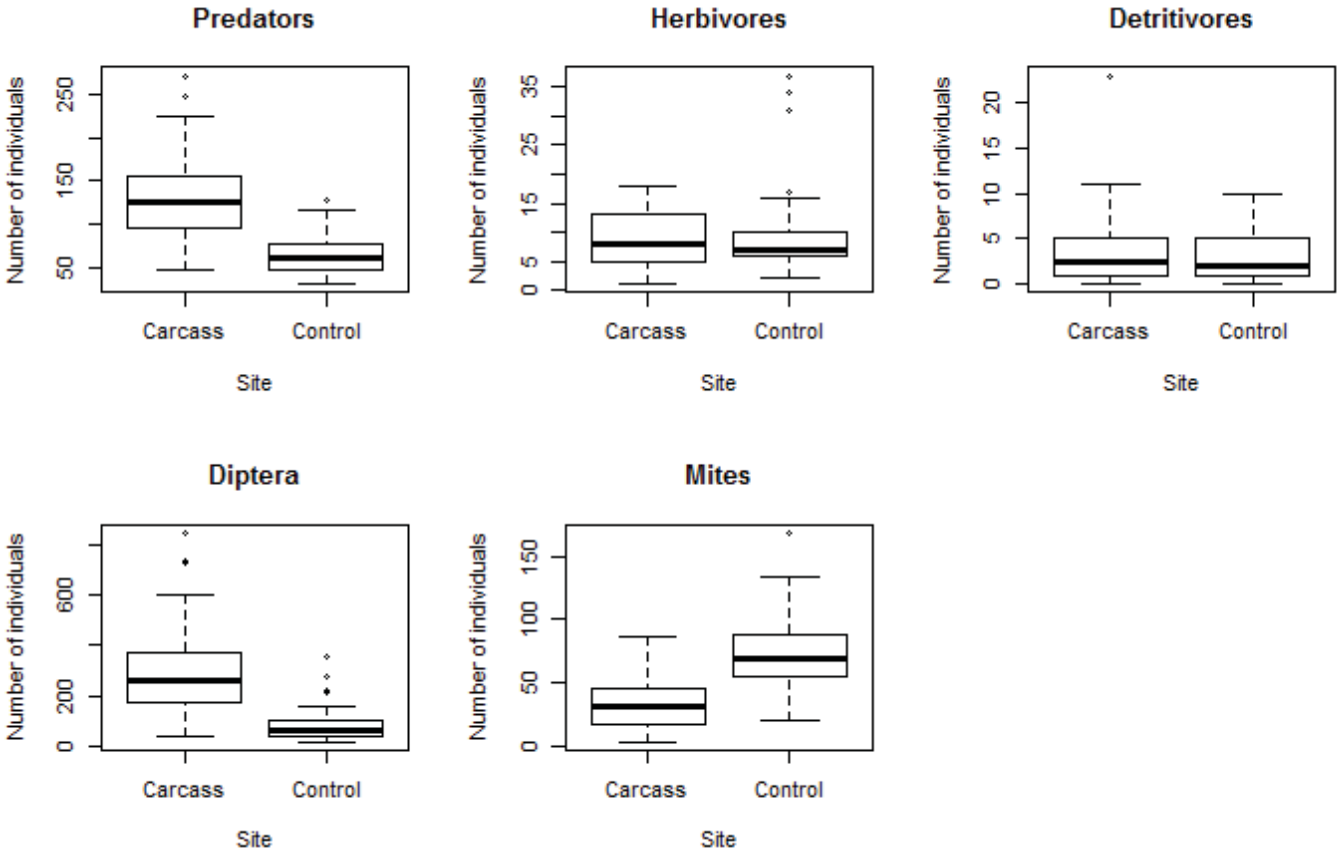

Figure 8: Boxplots showing the total abundance of the five main groups (predators, herbivores, detritivores, Diptera *and mites) in Hardangervidda 2018, in both the carcass site and the control site. Circles outside the boxes represent outliers. Whiskers represent 95 % confidence intervals, while the solid black lines represent the median.*

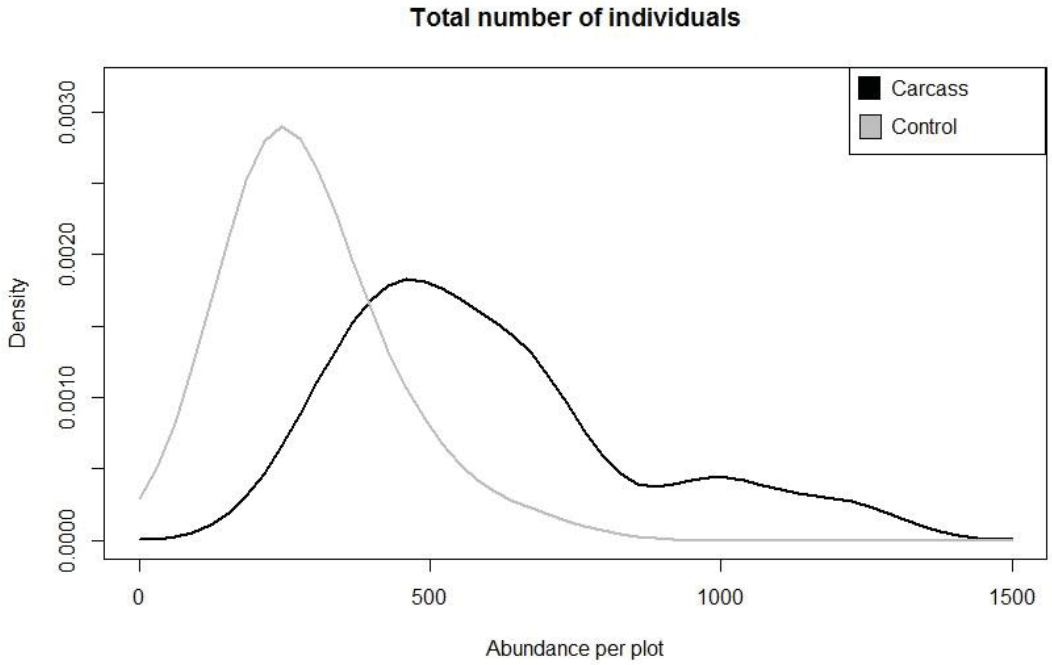

Figure 9: Density distribution plot for the total number of individuals caught in the pitfall traps in Hardangervidda 2018. Included here are the data from the 30 pitfall traps in the carcass site (black line, N=30) and the control site (grey line, N=30), a total of 60 traps.

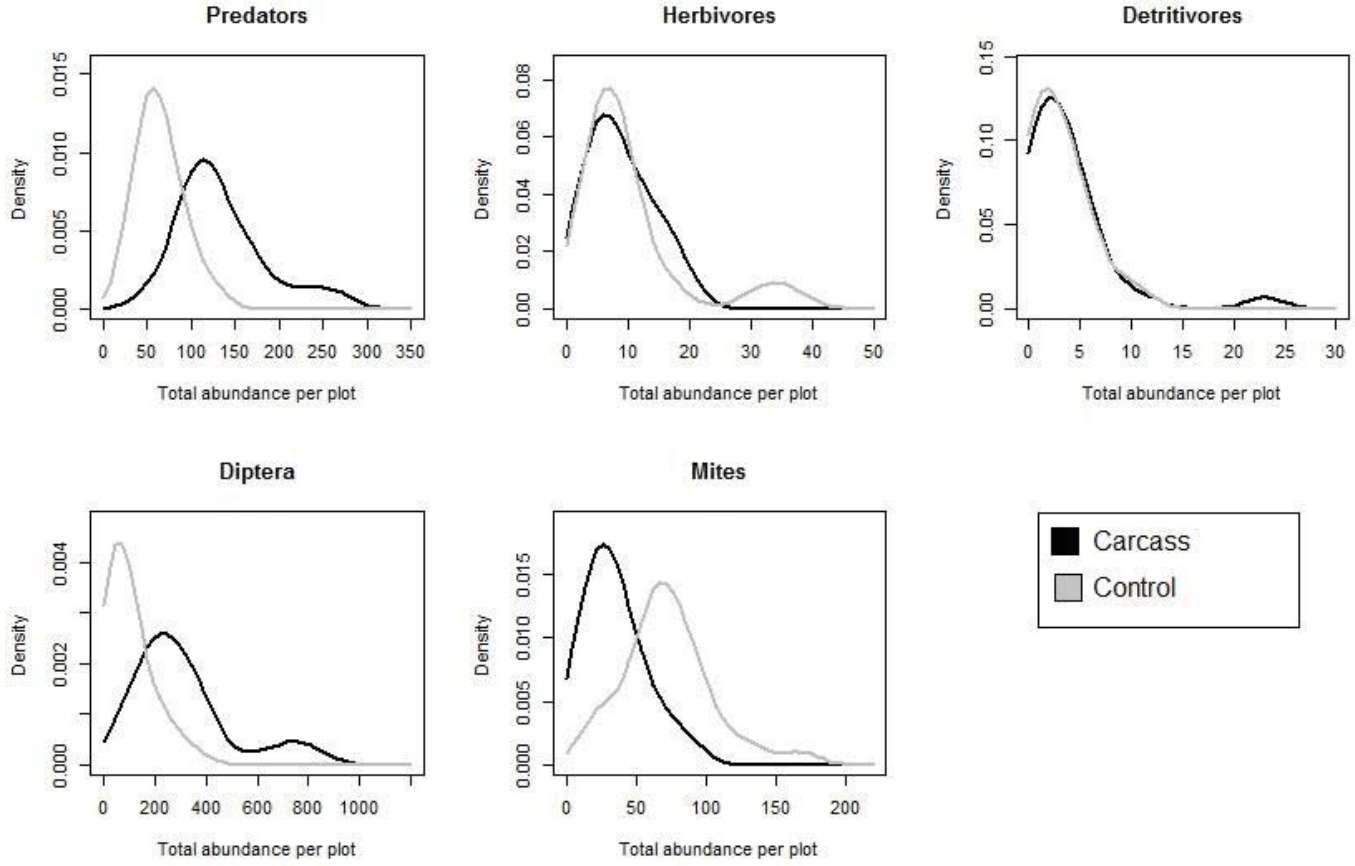

Figure 10: Density distribution plot for the five main groups caught in the pitfall traps in Hardangervidda 2018. Included here are the data from the 30 pitfall traps in the carcass site (black line, N=30) and the control site (grey line, N=30), a total of 60 traps.

The measure of abundance based on the sticky traps showed that they mainly consisted of *Diptera*, confirming their great abundance in the area. No blowflies were found. However, the surface area of traps covered with insects, which can act as a proxy for total biomass, was much higher in the carcass site (Figure 11, Fisher's exact test for count data yielded a p-value lower than 0.001).

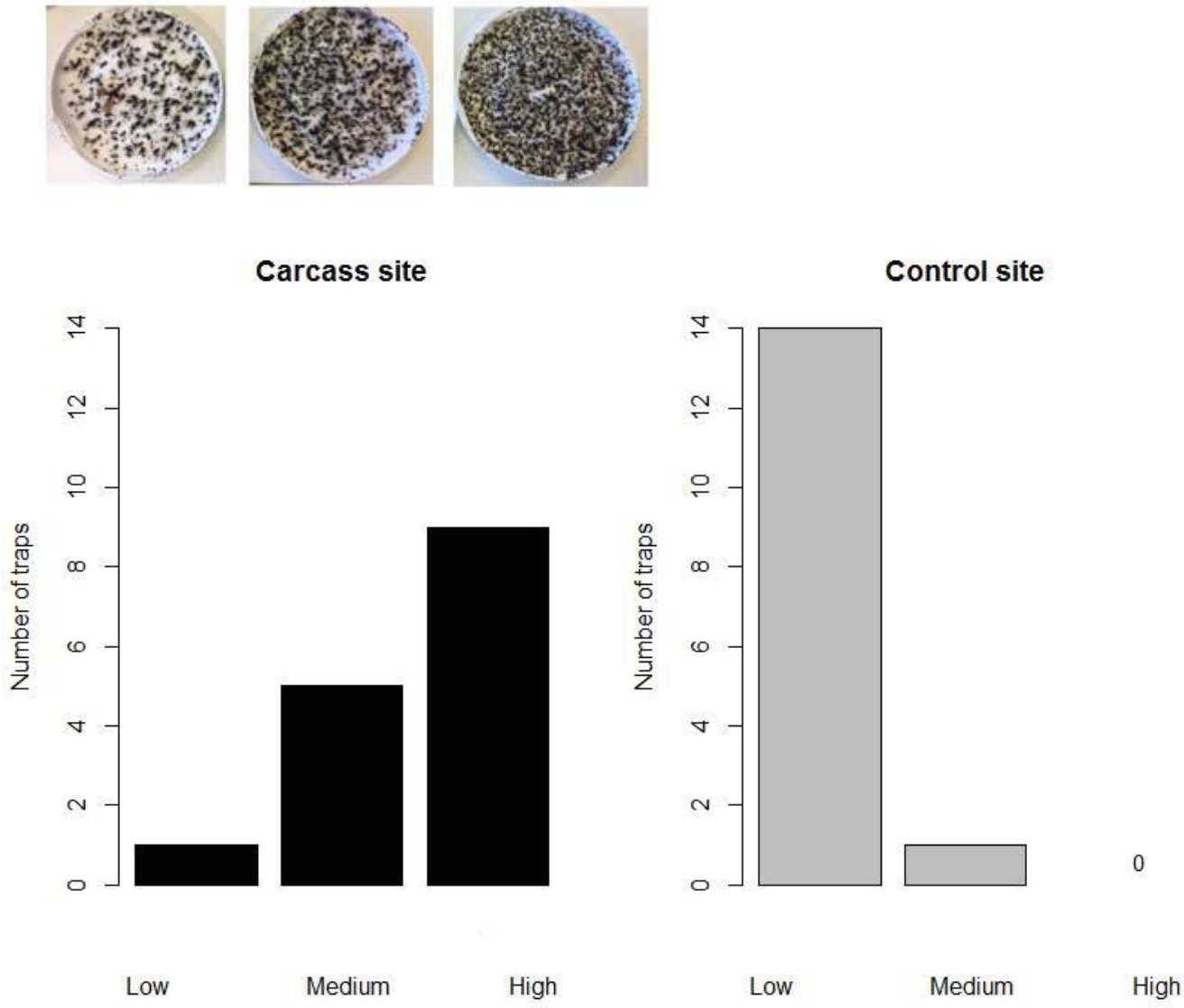

Figure 11: Shows the distribution of the sticky traps sampled in Hardangervidda 2018, according to coverage level of flying insects. The figure includes the distribution for the traps placed in both the carcass site and the control site (N=30). Also included in the figure are examples of the different coverage levels. Photos by Heidi Mørkhagen Granum.

3.1.2. Diversity

There was no significant difference in the Shannon's Diversity Index between the carcass site and the control site, although the numbers were close to significant (Figure 12, Table 9. Estimate: 0.08963, std. error: 0.04792, p-value: 0.0664). The diversity index for each individual pitfall trap can be found in Appendix 1, Table S5.

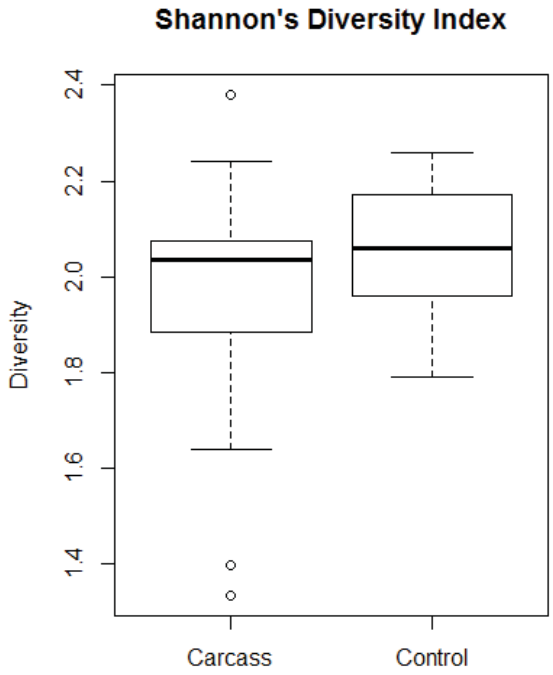

Figure 12: Boxplot showing the Shannon's diversity index for plots in the carcass and control site at Hardangervidda 2018 (N=60). Circles outside the boxes represent outliers, whiskers show the 95 % confidence interval and the black solid lines represent the median. There were no significant difference in the diversity between the two sites.

3.1.3. Taxonomic composition

The ordination plot below (Figure 13, top panel) shows how the taxonomic composition of predators, *Diptera* and mites differ between the control and carcass site (bottom panel). Predators and *Diptera* are associated with the carcass site, while the opposite is true for mites. From this plot we can also see that most predator groups tend to be found near other predator groups, which mean that they are often found in the same pitfall trap. This suggests that in the carcass site, a higher number of several predator species are found in one place. With a permutation test, the carcass and control plots are clearly separated ($p < 0.001$, Figure 13, bottom panel).

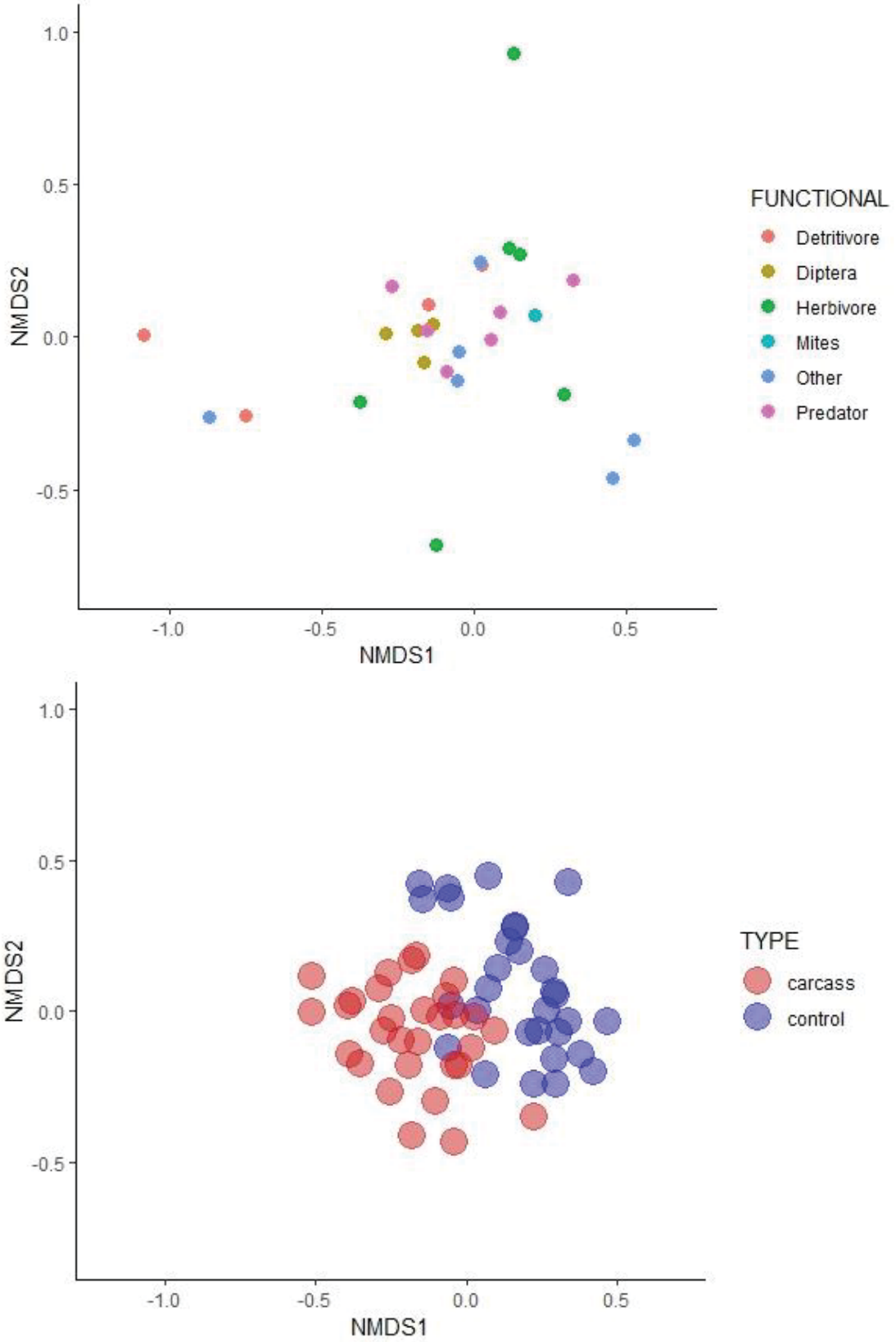

Figure 13: Ordination plot showing how the different taxonomic groups are associated with either one of the two sites (Carcass/Control, right panel), and how they are related to the presence of other taxonomic groups. This plot was composed after running Non-metric Multidimensional Scaling (NMDS). A permutation test also yielded a low p-value ($p < 0.001$), meaning that the carcass plots and control plots are clearly separated (left panel). From this plot, it is clear that predators and Diptera *are associated with the carcass plots, while mites are more associated with the control plots.*

3.1.4. Coleoptera indicator species

The beetles was the only taxa in which individuals were classified to the species level, and therefore the indicator species function applies only for *Coleoptera* species. The number of *Coleoptera* indicator species was three times higher in the carcass site (9) compared to the control site (3)(Table 3). Out of the 9 indicator species for the carcass site, the majority are predatory (only 3 were not).

Table 3: Coleoptera indicator species for the carcass and control site at Hardangervidda, 2018. There are three times as many indicator species in the carcass site compared to the control site. Ind. value is the indicator value of the species, while Freq is the number of times the species was present among the total of 60 samples (pitfall traps, N=60).

Species	*Site*	*Ind. value*	*P-value*	*Freq*	*Group*
Quedius fulvicollis	Control	0.418	0.002	15	Predator
Cryptophagus setulosus	Control	0.372	0.045	25	Omnivores/others (Fungi-eating)
Amara alpina	Control	0.333	0.002	10	Predator
Lesteva monticola	Carcass	0.873	0.001	37	Predator
Otiorhynchus nodusus	Carcass	0.790	0.001	38	Herbivore
Anthophagus alpinus	Carcass	0.700	0.001	58	Predator
Carabus problematicus	Carcass	0.700	0.001	32	Predator
Eucnecosum brachypterum	Carcass	0.690	0.001	34	Predator
Atheta aeneipennis	Carcass	0.430	0.004	20	Predator
Acidota quadrata	Carcass	0.345	0.001	12	Predator
Thanatophilus lapponicus	Carcass	0.242	0.020	9	Detritivore
Atheta altaica	Carcass	0.167	0.050	5	Predator

3.2. Small scale effects

3.2.1. Abundance and distance to carcasses

The total number of individuals per pitfall trap did not differ significantly with distance to the nearest carcass within the carcass site, and the distance was not important for the diversity index (Table 4). Only predators showed a significant change with distance to nearest carcass, while the results were close to significant for the detritivores (Figure 14, Table 4). Both predators and detritivores increased in numbers towards carcasses.

Table 4: Model results to assess the effect of distance to the nearest carcass in relation to the Shannon's diversity index, the total number of individuals, and for each of the five main groups. GLM with a negative binomial fit (family=Gaussian for the diversity index only) were run in R, based on the arthropods caught in the pitfall traps.

	Estimate	*Std. Error*	*P-value*
Shannon's diversity index	-0.005	0.021	0.818
Total number of individuals	0.002	0.012	0.989
Total number of predators	-0.022	0.010	**0.029**
Total number of herbivores	-0.012	0.017	0.471
Total number of detritivores	-0.055	0.031	0.075
Total number of Diptera	0.005	0.018	0.785
Total number of mites	0.009	0.019	0.613

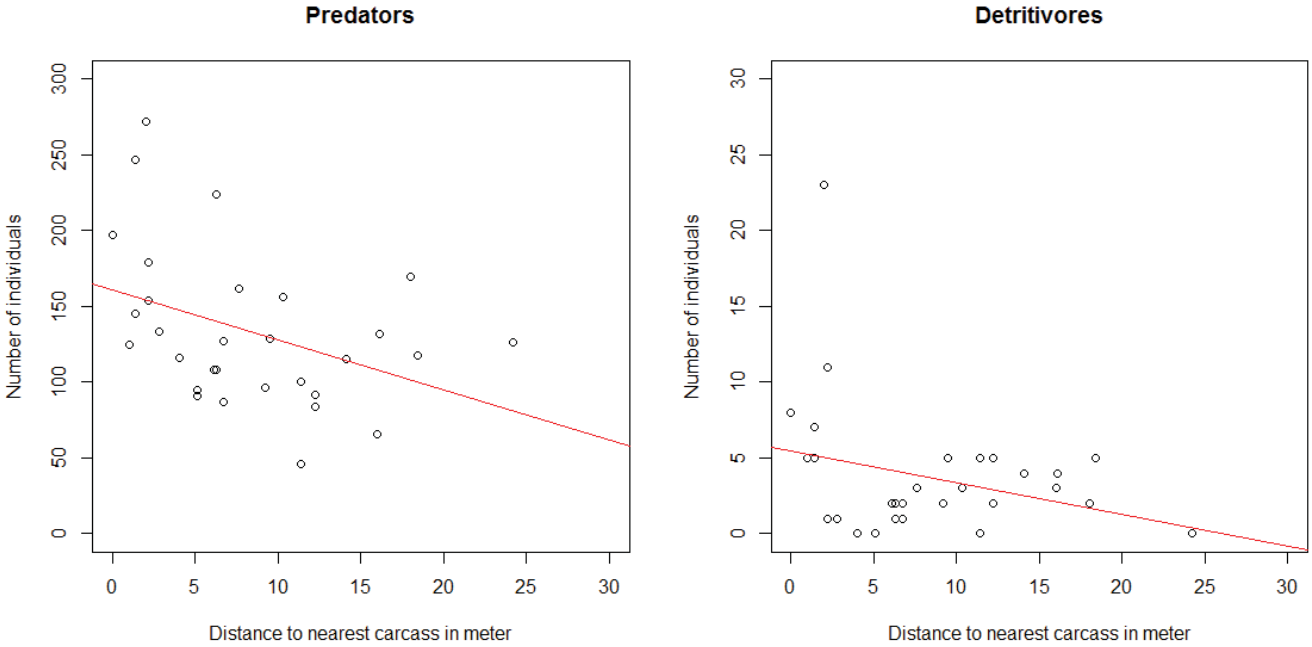

Figure 14: Scatterplots showing the number of predators and detritivores captured in each pitfall trap in the carcass site (N=30) in Hardangervidda 2018, and the response to the distance to the nearest carcass. We can see that there is a trend towards fewer predators and detritivores when moving further away from a carcass.

4. Discussion

As predicted, I found that the total number of arthropods were higher in an area two years after a mass die-off of reindeer compared to a similar control site nearby. The numbers of predators and *Diptera* were higher in the carcass site compared to the control site, and the opposite was true for mites. The number of herbivores and detritivores did not differ significantly between the two sites. This is partly as predicted, as predators were predicted to be affected by the large scale effects, but detritivores and herbivores did not respond as expected. The number of predators increased towards the carcasses within the carcass site as predicted, and the detritivores showed a similar trend.

The higher number of arthropods in the carcass site is equivalent to other studies that have found a higher number of individuals at carcass sites as compared to control sites (Melis et al. 2004, Sikes 1994). However, the Shannon's diversity index did not differ significantly between the carcass site and the control site. The reason is probably the higher evenness of functional groups in the control area. In the carcass area, there were a very high number of certain functional groups (e.g. *Diptera*), while the control area seemed to show a more stable community were each functional group had a more even number of individuals. Thus, there were more individuals in the carcass site, but this does not mean that the diversity index has to be higher. Similar results were found on the diversity indices in the studies done by Melis et al. 2004 on *Coleoptera* species on carcasses in a Norwegian forest. Important to mention is that the diversity index might have yielded different results if calculated on species level rather than higher taxonomic levels.

The higher number of individuals in the carcass site was mainly due to the increased abundance of *Diptera*, spiders, and rove beetles. The number of predators in general was more than doubled in the carcass site compared to the control site. It is likely that the increased numbers are because of more available prey in the carcass site, due to the very high numbers of *Diptera*. Many of these *Diptera* species feed directly on the carcasses, such as some *Cyclorrhapha* species, while others do not, such as *Sciaridae* species. Gu et al. 2014 found many arthropods on the carcasses in their study that are not immediately thought to be associated with carcasses or decomposition (Appendix 1, Table S2). A large proportion of the

Diptera were *Sciaridae*, species of which the larvae feed on fungi or decomposing plant material and the adults do not feed. Given that I only collected adults of the *Sciaridae*, they probably stayed in the carcass site where they hatched to breed. It is possible that these larvae utilize the dead plant material that is enriched with nutrients from the carcasses, and that the carcasses in this matter can be considered a driving force for adult *Sciaridae* when it comes to depositing their eggs. The rest of the *Diptera* were mostly *Cyclorrhapha* and *Orthorrhapha*, which were also observed on carcasses of roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), European badger (*Meles meles*) and mouflon (*Ovis orientalis*) in Germany (Gu et al. 2014).

Left out in many previous studies are *Arachnida* species, but based on the knowledge that most Arachnids are predator species, one can expect that the species found on and near carcasses are hunting the insects present. Even though many papers show increased insect activity and species richness near carcasses, the opposite was true for a cadaver of guinea pig (*Cavia porcellus*), where the author found decreased abundance of *Collembola* and *Acari* species (Bornemissza 1957). This is equivalent to my results, where the number of mites where significantly higher in the control site. Most of these mites feed on plant derived material, and it is possible that the lack of abundant plant life in the carcass site causes these mites to be more abundant in the control site.

The *Diptera* and mites were both affected by the presence of carcasses. On a small scale, however, there seemed to be little variation, meaning that the distance to the carcasses was of little importance. This can be explained by the fact that these carcasses are positioned on a hillside, where the run-off from the carcasses will affect a larger area surrounding each carcass. This means that areas that are not in close proximity to a carcass will still be affected if there is a carcass uphill from the area. Less mobile groups such as mites will then be affected regardless of their position in the carcass site, and the run-off from a carcass can be toxic, causing the overall numbers of mites in the carcass site to decline. There is an interesting interaction between the death of plants, the increase in *Sciaridae* species, the increase in predators and the decrease of mites. It could be possible that the increasing number of predators also have an effect on the abundance of mites, keeping their numbers

low. The death of plants seems to favor the *Sciaridae* species, but also have a negative impact on mites, while increased *Sciaridae* species favors the predators.

The indicator species function for the *Coleoptera* species indicated that three times as many species were associated with the carcass site when compared to the control site, showing that the carcass site is highly attractive and favors certain species. This is similar to the study done by Melis et al. 2004, where the abundance of *Coleoptera* species differed in both count and species between a carcass site and a control site. Given that nearly all the indicator species for the carcass site were predators, these results suggests that they are present because they hunt the increased abundance of prey species in the carcass site compared to the control site. When it comes to the small scale effects, the distance to the nearest carcass was not important for the total number of individuals captured in the carcass site. The majority of the individuals captured here was not part of a functional groups that is normally associated with carcasses, e.g. *Diptera.* However, the distance to carcasses significant affected predators, giving an indication that they are centered around and on the actual carcass when they hunt, for example for larvae and adults of *Diptera* species. Detritivores also showed a trend of increased abundance closer to the carcasses, showing that decomposing species indeed prefer to stay close to the actual carcasses.

There were no significant differences in the abundance of detritivores when comparing the carcass and the control site. This is likely due to the time delay of two years, as the reindeer carcasses were already in the dry stage of the decomposition process at the start of the fieldwork (stage dry/remains). Therefore, little nutrients and soft tissue was available for decomposing species to deposit their eggs. There were also no significant differences in the abundance of herbivores when comparing the two sites, which was unexpected. Hardangervidda has a relatively species-poor plant community, and the numbers of herbivores are generally low compared to the other functional groups. The herbivores are most likely to feed on plants outside the cluster of carcasses, as many of them were more mobile than mites and therefore not prone to the same effects of carcasses as the mites. It is also possible that the plants that act as food for the herbivores was less affected by the carcasses. Furthermore, most herbivores captured were adults.

Overall, the sticky traps had a higher cover of *Diptera* in the carcass site compared to the control site, and the *Diptera* also covered the majority of the sticky traps in a relatively short amount of time in the carcass site (personal observation), making many of the traps saturated and unable to capture individuals of other taxonomic levels. The high coverage on the sticky traps in the carcass site underlines the findings in the pitfall traps, where *Diptera* numbers were three times as high in the carcass site compared to the control site.

These results clearly show that large vertebrate carcasses affect the local species abundance, but not necessarily the species richness after a time delay of two years in a Norwegian alpine environment. The high number of arthropods will most likely have a profound bottom-up effect on a wide range of organisms and communities, as arthropods are a key prey species for many species of birds, for example Meadow Pipit (*Anthus pratensis*), Northern Wheatear (*Oenanthe oenanthe*), Bluethroat (*Luscinia svecica*), Common Reed Bunting (*Emberiza schoeniclus*) and Lapland Bunting (*Calcarius lapponicus*) for Harangervidda specifically. These birds were feasting on the abundant arthropod life at the same carcass site at Hardangervidda (Badia et al. In press).

Carcasses attract arthropod prey and induce a disproportionately higher predatory response of arthropod predators, due to higher efficiency because of less search effort. Thus, the carcass itself can act as a stronger attractant of arthropod predators than arthropod prey species alone, because the prey species are also attracted to the carcass. The high numbers of arthropod predators in the year of my study is also possibly because of effective and high reproduction in the previous year. This can change rapidly as the nutrition is being utilized, and a follow-up study is highly recommended to further investigate how long a mass death incident can continue to affect the local arthropod community in the alpine tundra and other ecosystems.

5. Conclusions

In this study, I have shown that mass death of reindeer may double arthropod abundance even two years after animal death. The arthropod increase was mainly due to the increase in predators as well as the mixed feeding *Diptera* groups. Whereas the predators are likely to find more prey close to the carcasses, the mechanism behind the *Diptera* increase is not fully understood. As plants are known to be negatively affected by carcasses, the lack of response by herbivores were unexpected. However, the lower number of mites may reflect the toxic effects of nutrient addition on a smaller scale. The species diversity was not different in the two sites.

The large scale effects (comparing results from carcass vs. control site) were far more prominent in this study than the small scale effects (comparing results within the carcass site). However, the distance to carcasses seems to be of importance for the abundance of predators, and to some degree detritivores.

The results in this particular study stress the importance of carrion as a long time provider of nutrition, not only for the arthropod community, but also for other animals in the food web, such as insectivorous birds and mammals. Carcasses thus have a profound bottom-up effect when it comes to other trophic levels, and further research in this particular field can help us broaden our knowledge to best protect cadaveric resources and the species which depend upon them in alpine environments.

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Appendix 1

Supplementary material

Table S1: The six stages of decomposition as proposed by Payne (1965) and the processes and species involved in each stage adapted from Grassberger and Frank 2004. Based on carcasses in terrestrial ecosystems that undergo decomposition directly on the soil surface.

Stage	Process (Simple)
Fresh	Blowflies colonizes the carcass to find a suitable site to lay their eggs. Blowflies can be seen within minutes, and the first eggs are laid after a couple of hours.
Bloated	Microorganisms releases gases inside the carcass, resulting in the bloating. Species such as house flies, hoverflies, flesh flies and black scavenger flies can be found at the carcass in addition to high numbers of blowflies.
Active decay	Maggots of blowflies feeding results in rapturing of the skin. Maggots reach their peak activity, and the carcass experiences rapid mass loss. Species of hymenopterans, ants, and scavenger beetles can be observed.
Advanced decay	The maggots pupate. Increased concentration of carbon and nitrogen in the soil. The carcass has lost most of its mass. Larger number of beetles are present. Dipterans other than blowflies increase in numbers.
Dry	Increased plant growth around the edge of the carcass. Parasitoid wasps can be observed. Rove beetles and carrion beetles dominate.
Remains	Increased plant growth within the carcass. Species composition as above, but in decreasing numbers.

Table S2: Some taxonomic groups found on carcasses and their function as described by Gu et al. 2014. This study was done on large carcasses in Germany. Excluded in this study are orders of Coleoptera *and class* Arachnida*. Pictures are retrieved from Google (labeled for reuse).*

Order	Function
Lepidoptera 	Sucking nutrients from decomposing carcasses
Hymenoptera 	Hornets hunting blowflies near and at carcasses, but also feeding directly on carcasses, creating tunnels. Bees sucking nutrients from carcasses. Ants feeding directly from carcasses.
Hemiptera 	Sucking nutrients and feeding on fresh carcasses
Collembola 	Opportunists in the soil beneath and around carcasses
Orthoptera 	Feeding on carcasses and fly eggs on carcasses
Diptera 	Adult blowflies lay egg in the carcass. Maggots feeding on and pupate in carcasses. Adults of some species feed on carcasses

Table S3: Summary of traps in the carcass area and the control area in my study on Hardangervidda 2018. In the carcass area, there is a gradient of carcass density, as there is a cluster of carcasses within my study area.

	Carcass area	Control area
Pitfall traps	30	30
Sticky traps	15	15
Gradient	Yes (carcass gradient)	No

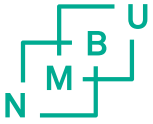
Table S4: Shows the taxonomical groups included in the total number of individuals for each of the five main groups and omnivores/others used in the statistical analyses in this thesis. The functional group number is the total of all the taxonomic groups included.

FUNCTIONAL GROUP	TAXONOMIC GROUPS
PREDATORS	Carabidae, Lycosidae, Thomisidae, other Arachnids, Ichneumonoidea, Staphylinidae
HERBIVORES	Byrrhoidea, sapfeeders, moths, Plecoptera, Lepidoptera, Curculionidae, Bombus, Symphyta, Vespidae, Scarabaeidae, Zygaenidae, Apiformes
DETRITIVORES	Leiodidae, Calliphoridae, Silphidae, Sarcophagidae
DIPTERA	Tipuloidea, Cyclorrhapha, Orthorrhapha, Nematocera, Tachinidae
MITES	Acari
OMNIVORES/OTHERS	Opliliones, Cantharidae, Neuroptera, Collembola, Latridiidae, Siphonaptera, Cryptophagidae

Table S5: Shannon's diversity index calculated on the plot level for all traps in both the carcass site and control site in my study at Hardangervidda 2018. The diversity index was calculated using GLM (family=Gaussian).

Plot ID	Shannons Diversity Index	Plot ID	Shannon's Diversity Index
C1	2.154207	**Car1**	1.811123
C2	2.050667	**Car3**	2.379781
C3	2.117972	**Car5**	1.334919
C4	1.84071	**Car7**	1.87398
C5	2.215108	**Car9**	1.934579
C6	1.984586	**Car11**	2.056088
C7	1.821163	**Car13**	2.041924
C8	1.957433	**Car15**	2.188651
C9	2.255981	**Car17**	2.036318
C10	2.01668	**Car19**	2.028487
C11	2.217847	**Car21**	1.833147
C12	2.235281	**Car23**	2.005354
C13	1.789453	**Car25**	2.189336
C14	2.145793	**Car27**	1.932478
C15	2.1727	**Car29**	1.923081
C16	1.919155	**Car31**	2.059074
C17	1.974943	**Car33**	2.060491
C18	2.017092	**Car35**	2.107749
C19	2.198204	**Car37**	2.033234
C20	2.260369	**Car39**	1.639858
C21	1.959243	**Car41**	2.047029
C22	2.069078	**Car43**	1.884875
C23	2.169038	**Car45**	1.781446
C24	1.911133	**Car47**	2.239618

C25	2.01262	**Car49**	2.074416
C26	2.154435	**Car51**	2.064666
C27	2.04595	**Car53**	2.186016
C28	2.134149	**Car55**	1.398118
C29	2.212077	**Car57**	2.109697
C30	1.845963	**Car59**	1.914575



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway