# MASTER´S THESIS

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# Directed Seed Dispersal Towards Animal Carcasses by Scavengers in Central Norway

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# Abstract

Carcasses are important resources in nature and are often the basal level in food webs by redistributing organic matter in ecosystems. They can be as a pulsed food source for scavengers and other opportunistic species and can affect many ecological communities and soil processes. A carcass ability to kill plant life and make changes in the soil chemistry provides an opportunity for other plants to establish. Seed dispersal through ingestion and defecation by animals (endozoochory) is a mechanism with much research and it is established as an important process in nature. This study mains to assess if ericaceous species uses directed seed dispersal through ingestion and defecation towards individual animal carcasses by scavengers and other carcass users (directed endozoochory), and if this process happens regularly in nature. Which factors attract a potential disperser, defecation rates at different area and the regularity of feces that contain viable seeds should be investigated to enlighten the main objective.

The study area located in central Norway had 11 (i.e. 33 plots) sites investigated during summer and autumn 2019. The sites were purposely selected in areas with boreal forest and a high ungulate prevalence. At each site three plots in similar habitats were chosen to be control plot, carcass plot and disturbed plot, and it was conducted habitat analysis at each of the 33 plots. Wildlife camera traps were rigged to observe both control and carcass plots, and at the carcass plot an animal carcass were deployed. Scats were counted and collected at each plot, and seeds were extracted and placed in a growth chamber to assess their viability.

Animal groups known to utilize a carcass resource like omnivores (e.g. red fox *Vulpes vulpes*, and European pine marten *Martes martes*) and opportunistic groups like corvids (e.g. hooded crow *Corvus cornix* and Eurasian jay *Garrulus glandarius*) showed to have a large proportion of the visits at the carcass plots. Compared with groups known to have a vegetarian diet like cervids (e.g. moose *Alces alces* and roe deer *Capreolus capreolus*), who were more common at the control plot. A vast majority of the feces registered were found at the carcass plots, and the feces showed to regularly have viable seed. From those seeds, seedlings from *Vaccinium spp.* were clearly the most common seedling.

These findings provide evidence of the study’s main objective. The carcass itself proved to have the biggest attraction value for potential dispersers of ericaceous species. There was a higher defecation rate at the carcass plots than in the other plots, and the fact that viable seeds were common in scats with *Vaccinium spp.* being the most common. All these findings point towards that directed seed dispersal towards individual single carcasses happens regularly in natural environments. Directed endozoochory could prove to be an important way to maintain and/or increase biodiversity through a relatively unresearched method of seed dispersal.

# Contents

# 1. Introduction

Offal and wildlife carcasses are important resources in nature, and are often the basal level in food webs by redistributing organic matter in ecosystems (Benbow, Tomberlin, & Tarone, 2015). Carrion is typically as a pulsed food source for facultative scavengers, generalist predators and many other carcass users of various taxa (Blazquez, Sanchez-Zapata, Botella, Carrete, & Eguía, 2009; Cortés-Avizanda, Selva, Carrete, & Donázar, 2009; DeVault, Rhodes, & Shivik, 2003). Despite the fact that plants make up about 99 % of all dead organic resources in terrestrial ecosystems (Swift, Heal, Anderson, & Anderson, 1979), large mammal carcasses have a significant impact on their surrounding areas (Carter, Yellowlees, & Tibbett, 2007). Blázquez et al. (2009) showed, for example, that the golden eagle (*Aquila chrysaetos*) and common raven (*Corvus corax*) are utilizing more than 95 percent of the carcasses available in Sierra Espuña Regional Park in Southeastern Spain.

Carcasses, especially of larger animals create a gathering point for opportunistic species, such as facultative scavengers (Beasley, Olson, & DeVault, 2015). In a study from the Polish-Belarusian borderland, the probability of occurrence of red fox (*Vulpes Vulpes*), common raven and Eurasian jay (*Garrulus glandarius*) increased significantly within a proximity of 1 km to large ungulate carcasses (Cortés-Avizanda et al., 2009). Carcasses are essential for scavengers and affect many ecological communities and soil processes (Beasley et al., 2015; DeVault et al., 2003; Fuller, 1934). Decomposing carcasses kill plant life underneath and nearby carcasses due to abrupt changes in the soil chemistry, turning a carcass site into a bare patch of soil already early in the decomposition process (i.e. Carcass Decomposition Islands, CDIs) (Carter et al., 2007).

CDIs provide unique opportunities for other plants to establish during secondary succession (Barton et al., 2016; Bump et al., 2009; Steyaert et al., 2018; Towne, 2000), and may create a mosaic in the landscape with patches of altered soil chemistry (pH, nutrition, carbon) and increases vegetation heterogeneity, as well as genetic and biodiversity across the landscape (Carter et al., 2007; Steyaert et al., 2018). For example, Barton et. al. (2016) found that levels of phosphorus are up to eight times higher at soil impacted by intact kangaroo carcass than soil at unsullied control sites, as well as a borderline significant higher abundance of annual plants at carcass sites compared to control sites without carcasses (Barton et al., 2016). Still, decomposition and the ecological role of carcasses in ecosystems is currently underrated and carcass ecology comprises a scientific area about which little knowledge exists (Carter et al., 2007). The carcasses will create microhabitats of high fertility that leads to landscape heterogeneity (Carter et al., 2007). It is observed that leachate from carcasses beneath CDIs is penetrating the soil down to 40 cm, and it is penetrating the soil in lesser extent up to 2.2 m from the cadaver (Coe, 1978). CDIs increase the pH, carbon and the nutrients in the soil (Carter, 2005).

Several species utilize ericaceous species like *Vaccinium spp*., as well as carcasses. A generalist species like that may be disperser seeds of *Vaccinium spp*. over relatively long distances (Liebe, 2019). Many plants are specialists in terms of their ecological niche (Whittaker, 1965), and many different seed dispersal mechanisms have evolved (Howe & Smallwood, 1982; Whittaker, 1965). For example, seed with low specific mass are often adapted to float and disperse via water (hydrochory), or, some seeds are adapted to disperse with the wind (anemochory) (Howe & Smallwood, 1982; Stoner & Henry, 2009b; Vittoz & Engler, 2007), such as Ground pines (*Lycopodium sp.)* which can travel up to 330 km by wind (Schmidt, 1918). Others species disperse their seed without external help (autochory), and can for example propel seeds away with ballistic mechanisms or they can simply drop down seeds from the plant (barochory) (Howe & Smallwood, 1982; Stoner & Henry, 2009b; Vittoz & Engler, 2007). Seed dispersal through animals (zoochory) is common seed dispersal mechanism in terrestrial ecosystems zoochory is the collective term of both external and internal seed dispersal. The external dispersal of seeds is often that seeds attached to animal fur and feathers, and it is called epizoochory (Couvreur, Cosyns, Hermy, & Hoffmann, 2005).

Endozoochory implies seed dispersal through the digestive tract of animals, when seeds are consumed (intentionally or not) by animals, pass their gastrointestinal system, and released through defecation while remaining viable (Couvreur et al., 2005). Zoochory is considered as a predominant dispersal mode in nature (Couvreur et al., 2005; Steyaert et al., 2018; Stoner & Henry, 2009b). It is estimated that 51 to 98 percent of seed dispersal from canopy and sub-canopy trees in the Neotropical realm is spread through zoochory, with endozoochory as the most important dispersal mechanisms (Couvreur et al., 2005; Stoner & Henry, 2009a).

Berry producing ericaceous species like bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*) and crowberry (*Emprtrum nigrum*) are keystone species of the boreal forest (Nilsson & Wardle, 2005). These species typically reproduce through clonal, vegetative propagation (García-Rodríguez, Albrecht, Farwig, Schabo, & Selva, 2018; Persson & Gustavsson, 2001), and sexual reproduction is considered to be rare (Kürschner, Stech, Sim-Sim, Fontinha, & Frey, 2007). Clonal propagation can be very effective. For example, clonal propagation in huckleberry (*Gaylussacia brachycerium*) a species closely related to Vaccinium, can result in individuals that cover almost 2000 meters in diameter and reach ages up to 13000 years old (Cook, 1983). Clonal propagation has limitations in terms of dispersal distance and genetics, but endozoochory may overcome these limitations. In addition to clonal propagation, many ericaceous species produce massive amounts of berries that contain viable seed, which are considered as adaptations for endozoochory (Couvreur et al., 2005). Yet, seedlings of those species are rarely discovered in the wild, and sexual reproduction is considered to be extremely rare (Kürschner et al., 2007). There appears to be a mismatch between the energetic investment used in sexual reproduction and the outcome of the mechanism (Persson & Gustavsson, 2001). Small scale disturbances in addition to nutritious soil are needed for germination and establishment for *Vaccinium spp.* and other pioneer species, and CDIs may provide those opportunities (Bump et al., 2009; Persson & Gustavsson, 2001; Platt, 1975; Towne, 2000).

Both berries of ericaceous species like *Vaccinium spp*. and carcasses are being utilized by numerous of different scavengers and generalist predators. And those species have the potential of disperse these seeds over relatively long distances (Liebe, 2019). Previous research indicates that seeds of ericaceous are dispersed towards CDIs by facultative scavengers, and this circulating mechanism could be the key understanding sexual reproduction in ericaceous plants with predominant sexual reproduction (Bump et al., 2009; Towne, 2000). Steyaert et. al. 2018 documented this mechanism at an ungulate mass mortality event (N = 323 reindeer), but it remains to be tested if this mechanism also occurs towards individual carcasses and its commonness in nature.

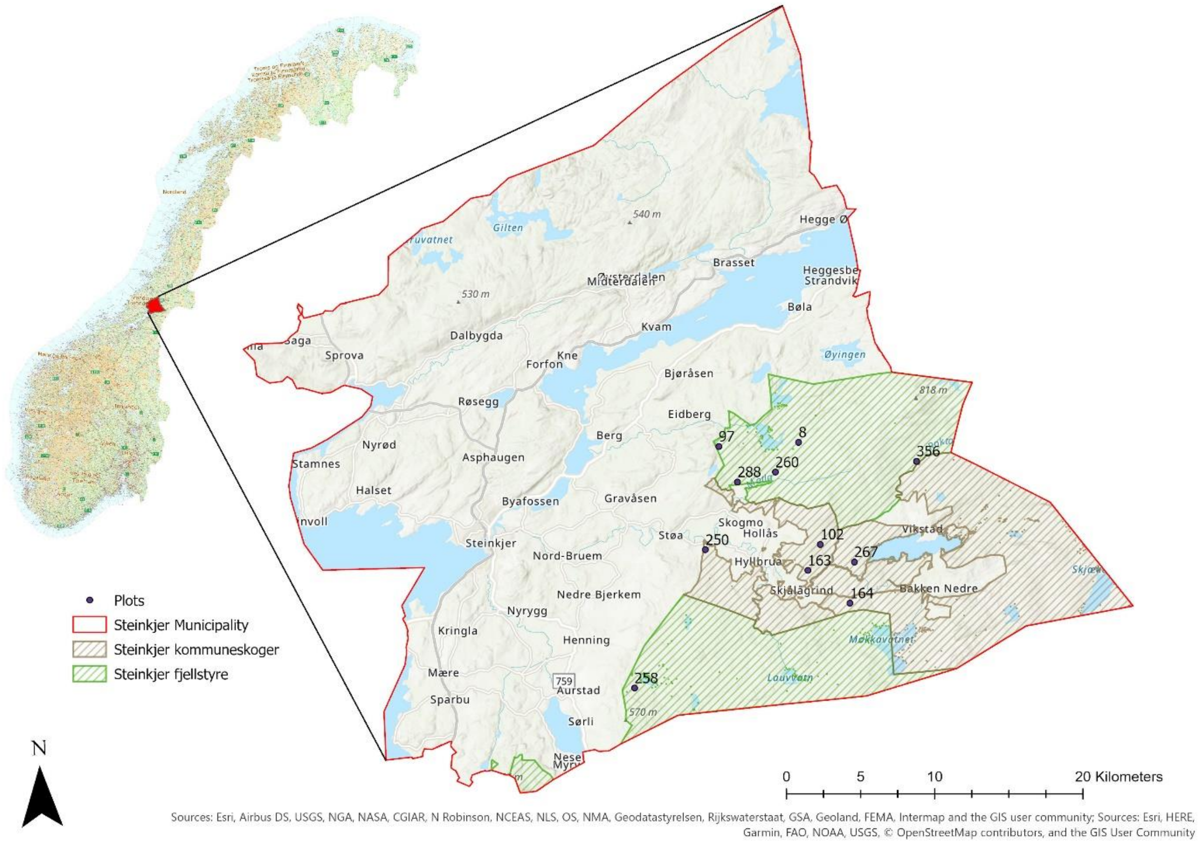
*Here, I hypothesize that scavengers and other carcass users disperse seeds of Vaccinium and other berry producing species towards individual animal carcasses through directed endozoochory.*

Three research questions are formulated to investigate and answer the hypothesis. 1) Potential disperses of ericaceous species attracted towards animal carcasses. 2) Defecation by potential dispersers are more frequent at carcasses than surrounding areas, and hence potential directed endozoochory. 3) Viable seeds of ericaceous species are regularly found in feces at carcasses.

# 2. Material and Methods

## 2.1 Study area

This study site is located in Steinkjer municipality in Central Norway (Figure 1) and, the area encompasses about 900 km$^2$ of mountain areas and forest. The forest is dominated by Norway spruce (*Picea abies*), but there is also a considerable amount of scots pine (*Pinus sylvestris*) and broadleaved species such as birch (*Betula spp*.). Different types of ericaceous plants dominate the forest floor, with bilberry (*Vaccinium myrtillus*) being the most common. Steinkjer holds a relatively high density of mesopredators and scavengers, such as red fox, European pine marten (*Martes martes*), several corvids and birds of prey (e.g. passerine (*Passeriformes*)), and ungulates such as moose (*Alces alces*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). The area experiences a high hunting pressure. For example, in the hunting season 2017-2018, 889 moose, 410 roe deer and 31 red deer were killed by hunters in Steinkjer municipality (1 565 km$^2$) (Statistics Norway, 2019a, 2019b, 2019c).



Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community; Sources: Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

*Figure 1:* Overview map of the study area, shows the location of Steinkjer municipality in Norway and where Steinkjer fjellstyre and Steinkjer kommuneskoger is located in the municipality. The placement of the 11 studied plots is illustrated. ArcGIS Pro 10.4.1.

## *2.2 Study design*

We generated 500 random points for establishing experimental plots, using ArcGIS Pro 10.4.1. The random points were restricted to forest areas inside Steinkjer Kommuneskoger and Steinkjer Fjellstyre (Figure 1), and outside a buffer area around roads (50 m) and buildings (100 m). All points were linked to several landscape variables, such as distance to roads (m) and buildings (m), slope (degree), aspect (cardinal directions), land cover type (forest), site quality class and dominating tree species (spruce, pine or broadleaf) to make an consistency, avoid unnecessary human disturbance and to choose favorable habitat for our research. Thereafter 11 points were selected manually according to efficiency (transportation time) in terms of distance and terrain.

At each site we selected three subplots, a control plot, a carcass plot and a disturbed plot, with 30 to 50 meters between each subplot. In the thesis 11 (i.e. 33 plots) sites were used, and all were visited and prepared in the summer 2019. The control plot and the carcass plot were rigged with motion triggered wildlife camera traps (Browning Spec Ops Full HD Trail Camera), and we conducted a vegetation and habitat survey at each subplot. We used a 1x1 $m^2$ frame (Figure 2) subdivided in 16 sub squares to register presence of all plant species (vascular, mosses, lichens), and estimated total cover (stone, soil, plant, mosses, lichens, carcass, litter) inside the frame according to Rydgren et. al. (2013). We used a metal chain to measure the microtopography (Appendix, Figure S1). We also categorized the patch size of similar vegetation to small, medium or large, and we used a relascope to count stem density of pine, spruce and broadleaved species. Furthermore, we investigated whether the site comprised a single or multi tree layer. Next, canopy cover was registered by using a densiometer (Lemmon, 1956), and a transect of 50 meters across the site was walked along which we counted all trees (pine, spruce and deciduous ) and estimated their height. We assessed vertical cover (i.e. sighting distance) by examining how far from the subplot a 50 cm long orange stick was visible from an average of the 4 cardinal directions (Appendix, Figure S2).

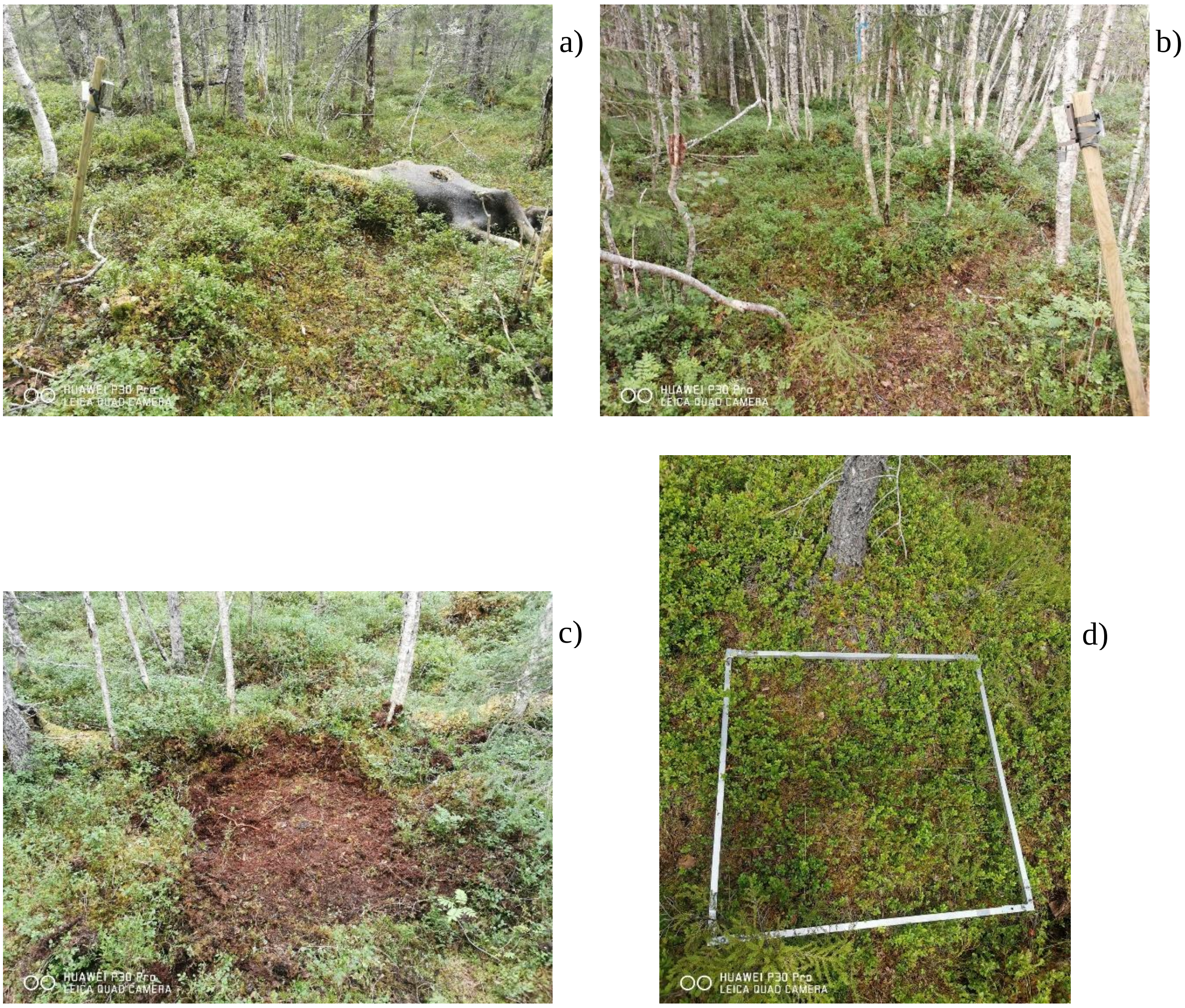


*Figure 2:* a) is displaying the carcass plot, b) is displaying the control plot, while c) shows the disturbed plot, all at plot 97. In picture d) we can see the 1x1 $m^2$ frame used at all the plots. Photos by Henry Køhler Haug.

Thereafter the sites were visited a second time during autumn 2019 to deploy carcasses at the carcass plot, to remove vegetation at the disturbed microsite, and to take two soil samples (a handful per sample) from inside the 1x1 $m^2$ frame at each plot. We got access to one intact moose, one red fox, two rabbits (*Oryctolagus cuniculus cuniculus*), and slaughter remains of seven moose (skin, head, entrails, legs, etc.) obtained during the annual moose hunt. For all carcasses, the weight was measured, dates of death and deployment, and cause of death were noted before being deployed (Appendix, Figure S3). A permission from Mattilsynet and the landowners were obtained with the requirement of a negative test for Chronic Wasting Disease (CWD).

The third visit, (average 20 days after carcass deployment) scats were counted and collected inside the 1x1$m^2$ frame (Appendix, Figure S4). All plots were investigated for four minutes

(15 seconds per subplot), and the scats were categorized in mammal, bird and rodent. Next, from the seeds collected they were separated from the scats, counted and categorized to which plot they were found at the school laboratory (Nord university), and inserted to a growth chamber (Model: KBW 720, Model version: KBW720-230V, Art. No: 9020-0340. 9120-0340). The seeds were placed in garden soil, and the growth chamber was adjusted to repeatedly swift between 12 hours days (light and heat) and 12 hours night (dark and less heat).

## *2.3 Camera trapping*

Our wildlife camera traps were placed at all control and carcass plots, the camera was placed four meters from the center of our plots. They were strapped to an impregnated wooden post at 1.2 meters above the ground, and the camera trap was placed south of the plot to avoid being blinded by the sun. The cameras were set to be triggered by motion, 3-shot standard (three pictures spaced three seconds apart) and a picture delay of one minute (one minute between each 3-shot). To organize the pictures from the 11 (i.e. 22 wildlife camera traps) plots the program Agouti was used. In Agouti we imported our picture data from our memory cards and the program provided us with an easy way of handling the material. The pictures were divided into sequences (one sequence per visit), and for each sequence a drop-down menu of species observed, and of their number could be selected from.

From the observations by the camera traps, the species were categorized both in potential Vaccinium dispersers and in functional groups. The following species could be considered as potential dispersers of *Vaccinium spp.*; red fox, European pine marten, European badger (*Meles meles*), stoat (*Mustela erminea*), common raven, hooded crow (*Corvus cornix*), Eurasian magpie (*Pica pica*), Eurasian jay, Siberian Jay (*Perisoreus infaustus*), thrush (*Turdidae*), and passerine (Hogstad, 2016; Ibañez, Andreucci, & Montalti, 2016; Liebe, 2019; Wenny, Sekercioglu, Cordeiro, Rogers, & Kelly, 2016). While the functional groups created were Cervidae, Rodentia, Carnivora, Accipitridae, Corvidae, Tetraonini and OtherBirds (Appendix, Table S1).

## 2.4 Statistical approach

For all statistical analysis RStudio 1.1.456 was used. Explanatory variables are listed in Appendix, Table S2, and regarding the data material there were two outliers. In the variable “Microtopography” and the variable “WeightKG”, that was removed to make the dataset more solid. It was also considered to be no collinearity based of the fact that that none of the correlation coefficients were higher than 0.6.

In the investigation of the first research question, i.e. to determine which factors influence a dispersers presence at the plots, regression analysis was used. A negative binomial regression was chosen with the abundance of “VacciniumDispersers” as the response variable, and “Type” and “CameraDays” as the explanatory variables (Appendix, Table S2). The model with those explanatory variables was chosen by model selection consisting 24 different candidate models. Thereafter an ordination plot (non-metric multidimensional scaling) was made to place the functional groups (Appendix, Table S1) in relation with “Type” at the plots, and the validation was performed with a stressplot (Appendix, Figure S5) (Oksanen, 2011). The three dimensional stressplot had a relatively small ordination distance of the observed dissimilarities (Oksanen, 2011). Model selection was using Akaike information criterion (AIC) diagnostics to choose the most fitted candidate model, by choosing the candidate with the lowest value (or close to lowest with less degrees of freedom) for all model selected.

To assess if the number of scats differed between the plots a mixed effect logistic regression (glmer) of the Poisson family was used (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To assess if defecation rates differed between the plots, I used a glmer analysis. The original count data (scat count per subplot) where changed to binomial data to be able to fit the model. Model selection were using AIC diagnostics as outlined before.

A binomial glmer was also used to test if the probability of finding scats correlated with carcass biomass. And because of overdispersion, I only report descriptive statistics for the seedload detected in scats and the number of seedlings that emerged from collected scat material.

# 3. Results

## *3.1 Dispersers presence at the plots*

Out of the 4193 (4011 at carcass plot and 182 at control plot) visits of 27 different species at the wildlife camera traps, 3985 (3884 at carcass plot and 101 at control plot) of these visitors could be categorized as Vaccinium dispersers (Appendix, Table S3).

The selected negative binominal regression model indicated that there were significantly more dispersers of Vaccinium species at the treatment type “carcass” than the treatment type “control” ($\beta = -3.8639$, s.e. = 0.4636, $p$-value < 0.0001). And that Vaccinium dispersers increase over time ($\beta = 0.1160$, s.e. = 0.0447, $p$-value = 0.0094). Predicted values of Vaccinium species in relation with treatment and number of camera days is showed below (Figure 3).

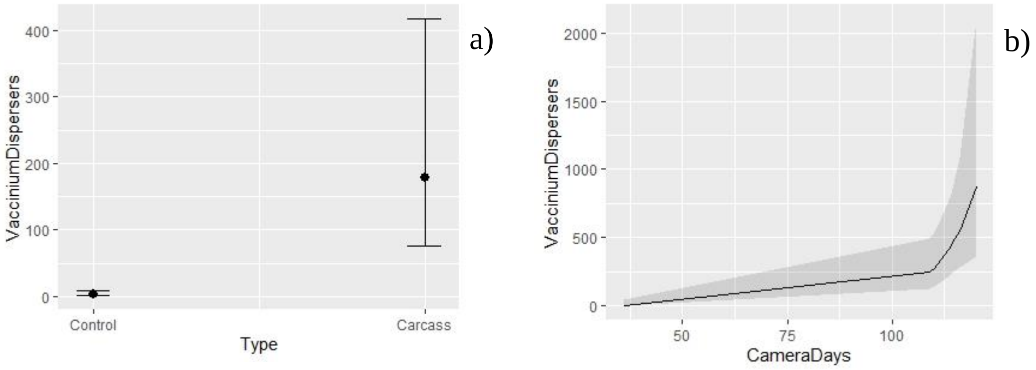


*Figure 3:* Predicted numbers of Vaccinium dispersers at the treatments types, control and carcass (a), and it is significantly more dispersers at the carcass treatment compared with the control treatment. (b) shows the predicted relation between Vaccinium dispersers and the number of camera days, the (b) figure indicates a positive correlation.

From all the variables that were measured at the plots (Appendix, Table S2), the treatment type was the only significant factor affecting the functional groups of visitors ($p$-value = 0.001). Most of the functional groups expected to disperse *Vaccinium spp.* by utilizing an animal carcass has a relation to the treatment type “carcass” (Figure 4). The stressplot shows a good validation of the ordination (stress = 0.0674) (Appendix, Figure S5).

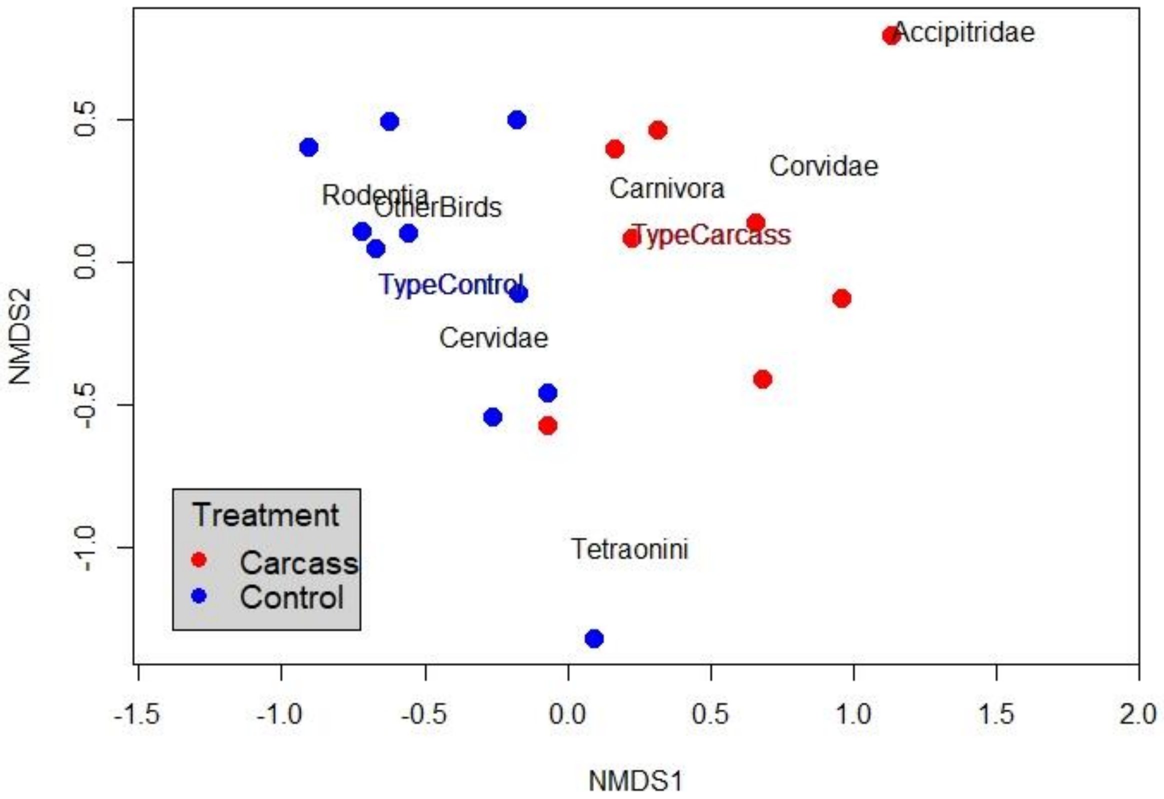


*Figure 4:* The non-metric multidimensional scaling (NMDS) ordination shows the placement of the different groups of species in relation with the treatment types, carcass (red) and control (blue).

## 3.2 Defecation rates at the plots

We found 181 scats at the carcass plots, three at control plots and six scats in disturbed plots, the carcasses were deployed between August 9 and October 9, 2019. The scats were sampled between October 4 and 25, 2019. In average the scats were collected about 20 days after carcass deployment. Seven of the scats were from mammals, while the remaining 183 scats were from birds. The binomial regression showed that the probability of finding feces per subplot were about 39 % at the carcass plot ($\beta = -0.4514$, s.e. = 0.5311, *p*-value = 0.3950), 1 % at the control plot ($\beta = -4.4246$, s.e. = 0.6307, *p*-value < 0.0001), and 1 % at the disturbed plot ($\beta = -3.8902$, s.e. = 0.5138, *p*-value < 0.0001) (Figure 5). The variance of the random effect was 0.000 for subplots and 2.6 for plots.

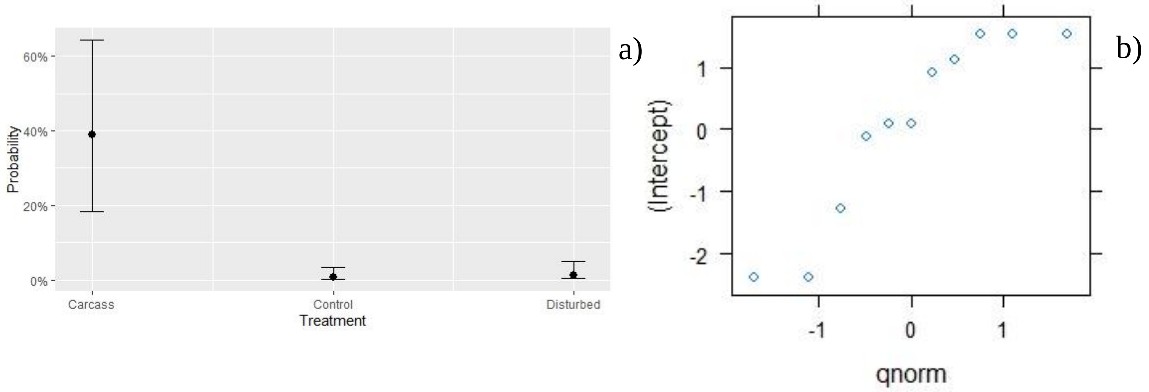


*Figure 5.* (a) The probability of finding feces per subplot, and (b) visualizing the variance of the random effect for (a).

The probability of finding scats in relation to biomass of carcass (kilograms) was positive (β = -2.6258, s.e. = 1.7175, p-value = 0.1260) (Figure 6). While the variance for subplot and plot were 0.3132 and 4.5773, respectively.

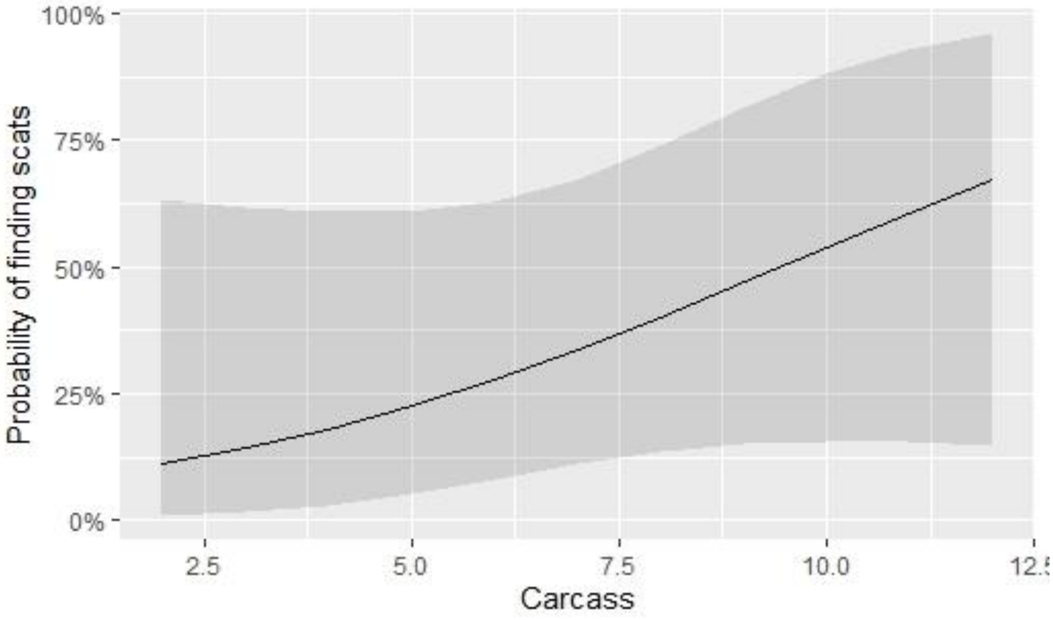


*Figure 6:* The probability of finding scats is increasing when carcass biomass in kilograms are increasing.

### *3.3 Viable seeds in the scats*

Like mentioned above 181 scats were registered, 38 of them were collected and 276 seeds were detected from them (Table 1). Out of these seeds, 61 seedlings germinated whereof 51 of the seedlings were from *Vaccinium spp.*

*Table 1:* The table is an overview of the scat collection. First it is Scat ID there the three first number indicates which plot the scat is from, and the fourth number indicates the scat sample. Species tells us where the scat comes from, while the weight column shows the weight of the scat. Thereafter, the tables show the number of seeds, seedlings and Vaccinium seedlings, before the table tells when the scat collecting took place and which species the carcass is.

| **Scat ID** | **Species** | **Weight** | **N seeds** | **N seedling** | **N Vaccinium seedling** | **Date collected** | **Carcass type** |
|---|---|---|---|---|---|---|---|
| 0081 | bird | 0,062 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 0082 | bird | 0,106 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 0083 | bird | 0,059 | 27 | 8 | 8 | 15.10.2019 | Alces alces |
| 0084 | bird | 0,262 | 5 | 2 | 2 | 15.10.2019 | Alces alces |
| 0085 | bird | 0,037 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 1631 | bird | 0,099 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 1632 | bird | 0,048 | 1 | 0 | 0 | 16.10.2019 | Alces alces |
| 1633 | bird | 0,006 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 1634 | bird | 0,087 | 2 | 0 | 0 | 16.10.2019 | Alces alces |
| 2501 | bird | 0,115 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 2502 | bird | 0,044 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 2503 | bird | 0,034 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 2504 | bird | 0,566 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 2505 | bird | 0,041 | 1 | 0 | 0 | 15.10.2019 | Alces alces |
| 2506 | mammal | 1,148 | 0 | 0 | 0 | 15.10.2019 | Alces alces |
| 2581 | bird | 0,297 | 56 | 13 | 13 | 17.10.2019 | Alces alces |
| 2582 | bird | 0,629 | 109 | 19 | 19 | 17.10.2019 | Alces alces |
| 2583 | bird | 0,087 | 15 | 3 | 3 | 17.10.2019 | Alces alces |
| 2584 | bird | 0,092 | 10 | 1 | 1 | 17.10.2019 | Alces alces |
| 2601 | bird | 0,04 | 4 | 6 | 0 | 21.10.2019 | Alces alces |
| 2602 | bird | 0,146 | 0 | 0 | 0 | 21.10.2019 | Alces alces |
| 2603 | bird | 0,131 | 2 | 1 | 0 | 21.10.2019 | Alces alces |
| 2604 | bird | 0,254 | 0 | 0 | 0 | 21.10.2019 | Alces alces |
| 2671 | mammal | 1,036 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2672 | mammal | 0,114 | 0 | 0 | 0 | 16.10.2019 | Alces alces |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| 2673 | bird | 0,084 | 2 | 0 | 0 | 16.10.2019 | Alces alces |
| 2674 | mammal | 0,028 | 37 | 5 | 5 | 16.10.2019 | Alces alces |
| 2675 | mammal | 0,287 | 2 | 2 | 0 | 16.10.2019 | Alces alces |
| 2676 | mammal | 0,225 | 2 | 0 | 0 | 16.10.2019 | Alces alces |
| 2881 | bird | 0,091 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2882 | bird | 0,049 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2883 | bird | 0,156 | 1 | 1 | 0 | 16.10.2019 | Alces alces |
| 2884 | bird | 0,161 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2885 | bird | 0,118 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2886 | bird | 0,07 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2887 | bird | 0,059 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 2888 | bird | 0,175 | 0 | 0 | 0 | 16.10.2019 | Alces alces |
| 3561 | bird | 0,071 | 0 | 0 | 0 | 21.10.2019 | Oryctolagus cuniculus cuniculus |

# 4. Discussion

This study is inspired by Sam et. al. (2018) research at Hardangervidda where a mass mortality event took place. The event gave the opportunity to study directed endozoochory towards carcasses, and to investigate if this mechanism happens regularly. Main objective of this thesis was to investigate whether or not directed endozoochory is a prevalent mechanism in nature. Therefore, three questions were investigated; 1) what caused dispersers to visit our plots, 2) what are the dispersers defecation rates at the plots, and 3) if their feces contain viable seeds. My study indicates that scavengers and carcass users indeed disperse seeds of ericaceous species toward animal carcasses. First, the variable most important to attract a potential disperser is the carcass itself. Second, clearly most feces found on the plots with carcass compared with the control plot and the disturbed plot. And third, the feces regularly contain viable seeds that germinated to *Vaccinium spp.*

This phenomenon of endozoochory has already been investigated other places around the world (Couvreur et al., 2005), but also in Hardangervidda in Norway (Steyaert et al., 2018). The main difference between the Hardangervidda project and our project is if the mechanism of endozoochory also exists at single carcasses and not only at areas with mass death. The lightning strike caused a mass death of wild tundra reindeer (N= 323) (Steyaert et al., 2018). It is obviously that a larger number of carcasses has a greater attraction value for species that utilize carcasses, but in our case, we managed to find evidence for it in a more natural environment. Another difference comprises the terrain and the vegetation, in Hardangervidda is less vegetated and alpine tundra while my study area is much more dominated by boreal forest.

In Couvreur et. al. (2005) study in the nature reserve “Houtsaegerduinen” in Belgium, they detected endozoochory for 53 species from their 6675 seedlings samples while in our project the mechanism was detected for six species from our 61 seedling samples. Worth mentioning is the difference of the size of the projects, the fact that Couvreur released donkeys and collected a large proportion of the scat samples from them and a general lower biodiversity in Norwegian forest areas (Nybø, Certain, & Skarpaas, 2012). In another study from Kilpisjarvi region in Finland (at the Norwegian border) they are showing a positive correlation between voles (the year after), and seed crop and flowering intensity of bilberries (*Vaccinium myrtillus*) in the subalpine birch forest zone (Laine & Henttonen, 1983). This could indirectly indicate zoochory between bilberries and voles.

When looking at which factors influence a potential disperser to visit our plots, the indisputable factor was the presence of a carcass. But I may be a bit strange that none of the habitat variables had an impact on the species community per site. A possible explanation is that the project is in the initial phase, only 11 plots could be used in this thesis. It is also worth mentioning that the distribution of the plots in a relative similar landscape was done purposely. Therefore, the habitat mosaic of the study area had a relatively similar terrain, vegetation and biodiversity, which means that there were not very large differences in the measured environmental variables. While in the prediction plot b) Figure 3, there was showed a positive correlation between "VacciniumDispersers" and "CameraDays". That implies the more days the cameras are active the more dispersers are detected, and in this case the explanatory variable is the number of camera days. This may be implying that the factor of human disturbance is important, the longer period of no disturbance the higher the visiting frequency gets.

I found that functional groups of species known to utilize meat resources were closely related to the carcass plots, whereas functional groups with a vegetarian diet tended to relate more to the control plots. It should be mentioned that the Rodentia group, that may be associated with carnivores, consists mainly of mountain hares and Eurasian red squirrels. The fact that carnivores etc. are more related to a carcass may be logical, but it also may imply that these functional groups are more important to ericaceous plants than expected. It shows that these groups may increase the biodiversity and change the habitat mosaic in nature by performing directed endozoochory. Thus, directed endozoochory increase of diversity both with movement of the seeds themselves and the fact that they can be spread over relatively long distances could make landscape more resistant against rapid changes. A landscape with a high genetic diversity is better prepared to adapt to changes compared to more monotone landscape (Schippers et al., 2015).

The defecation rates at the different treatment types were very different, I registered 181 (38 collected) scats at carcass plots, but only three at control plots and six at disturbed plots. This is most likely a result of the inequitable distribution of visits at the different treatment types. Another notable factor is the numeric difference between mammals and birds, six feces from mammals and 32 feces from birds. This can be explained by the fact that birds were more frequent at the plots in addition to birds high defecation rate compared with the mammals (Mitchell, Rowe, Ratcliffe, & Hinge, 1985). This also means that plant species preferred by birds may be more suited for directed endozoochory, and another fact is that birds have the potential to disperse seeds over longer distances than mammals. Carcass plots were the hotspots for defecation, which is an evidence of directed endozoochory and shows the importance of carcasses in nature. The carcasses are not only important for directed endozoochory, but also as a resource for the dispersing species. While figure 6 illustrate the positive correlation between probability of finding scats and biomass of carcass. The detection probability increases the more carcass biomass, contribute to strengthening the hypothesize that scavengers and other carcass users disperse seeds of Vaccinium and other berry producing species towards individual animal carcasses through directed endozoochory. Again, it shows the importance of the carcasses in nature, and it also visualizing the circle of life. For example, a mammal is benefiting of eating ericaceous species in its lifespan, that also may benefit the ericaceous by spreading it through endozoochory, and when the mammal die it will initiate directed endozoochory.

From the 276 seeds found in the scats, 61 seedlings appeared, of which the vast majority were *Vaccinium spp.* (84.6 %). That large proportion of the seedlings which most likely can be explained by how frequent *Vaccinium spp.* are in the study area in addition to them being a common food source for many of the species visiting the plots. About one-fourth (22 %) of the seeds turned out to be viable. Because of the large proportion of bird feces, comparing it to a study at Santa Cruz Island in Galapagos may give an insight of the commonness. In this study they collected feces from birds eating different fruits and their viable seeds ratio at 23 % matches mine at one-fourth relatively good (Guerrero & Tye, 2009).

Most of the data material is relatively unequal distributed because of the high attraction value the carcass plot has compared with control and disturbed plot. This has led to the fact that Poisson regression and negative binomial regression has been used in many of the statistical approaches due to their suitability to handle counts, unequal distributed and overdispersion data. And that points out the explanatory variables that is affecting our response variable.

The choice of wildlife camera traps to identify the potential Vaccinium disperser was a non-invasive and accurate method of collect data material. Which was the preferred way to avoid any unnecessary disturbance for the species living in the study area. For the field work we were two persons (master and phd students) that was guided be a professor in the beginning to make a standardized procedure to follow in the continuation of the work. Thereafter, in all the fieldwork at least one of the two of us were present at the fieldwork, but most of the time we both were in attendance. That was a purposely method to minimize sources of error.

# 5. Conclusions

Throughout this project that still is in an initial phase we have shown indicators of our hypothesis. That scavengers and other carcass users disperse seeds of ericaceous species, vaccinium species in our case, towards single animal carcasses. Looking at the research questions, all of them have been investigated and we have found verifications that may answer those questions. 1) What drives a potential disperser of ericaceous species towards our plots, a source of food. 2) If there are differences in defecation rates at our different treatment types, yes. The plots treated by a carcass deployment tends to have the highest rate of defecation. 3) Do the feces collected at the plots contain viable seeds, yes. About one-fourth to one-fifth of the seeds germinated to become seedlings.

This study could indicate that directed endozoochory is a natural mechanism species use to disperse their seeds, potentially over relative long distances in our study area in Central Norway.

Through the continuation of this project we may get more answers and stronger validation of our hypothesis. With more plots, more carcasses acquired and further work within the standardized field work procedure more knowledge will potentially prove our hypothesis to be strong and enlighten knowledge regarding endozoochory and carcasses as an important resource in nature.

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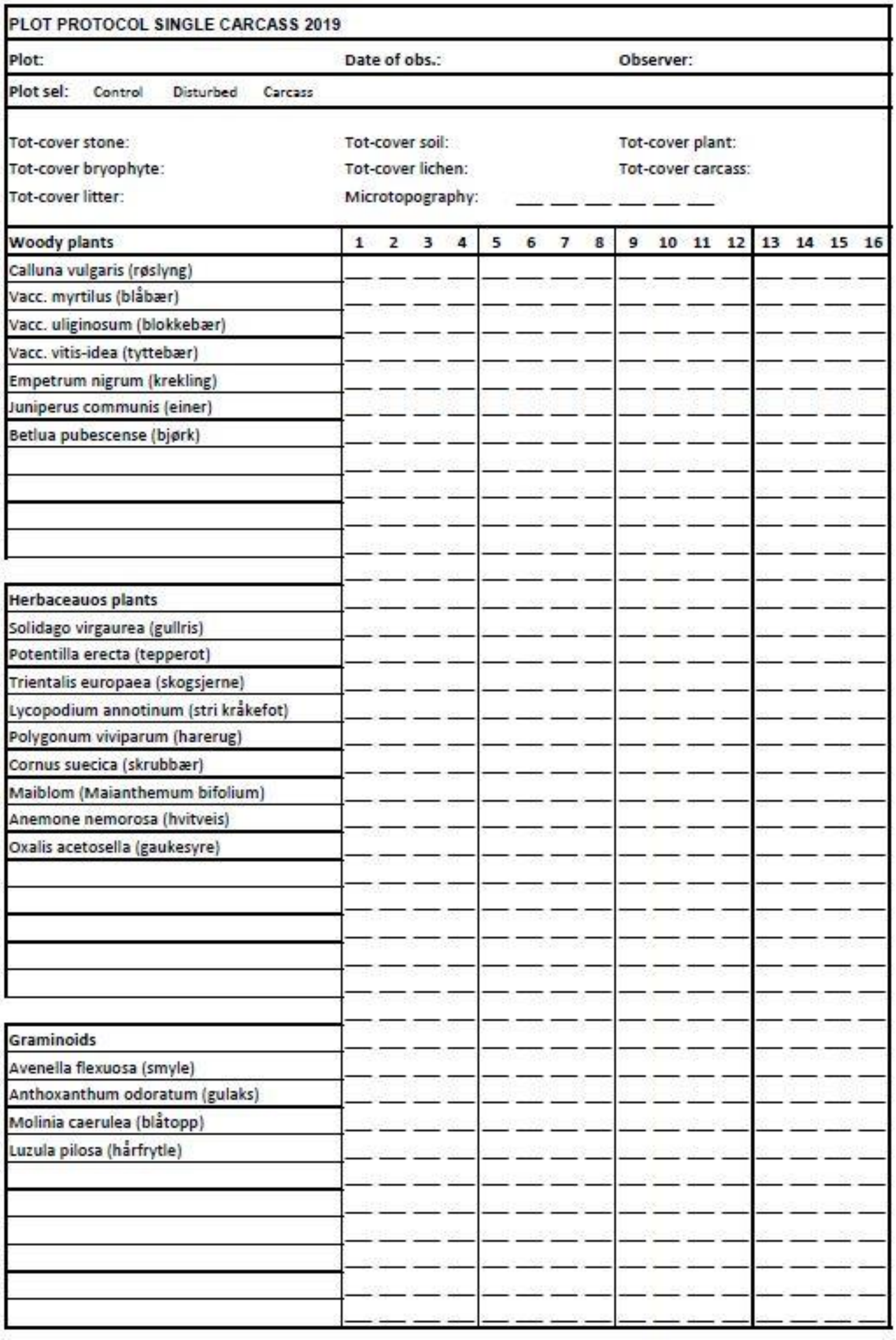
# Appendix

Supplementary material



PLOT PROTOCOL SINGLE CARCASS 2019

Plot: Date of obs.: Observer:

Plot sel: Control Disturbed Carcass

Tot-cover stone: Tot-cover soil: Tot-cover plant:
Tot-cover bryophyte: Tot-cover lichen: Tot-cover carcass:
Tot-cover litter: Microtopography: ___ ___ ___ ___ ___ ___ ___

| **Woody plants** | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
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| Calluna vulgaris (røslyng) | | | | | | | | | | | | | | | | |
| Vacc. myrtilus (blåbær) | | | | | | | | | | | | | | | | |
| Vacc. uliginosum (blokkebær) | | | | | | | | | | | | | | | | |
| Vacc. vitis-idea (tyttebær) | | | | | | | | | | | | | | | | |
| Empetrum nigrum (krekling) | | | | | | | | | | | | | | | | |
| Juniperus communis (einer) | | | | | | | | | | | | | | | | |
| Betlua pubescense (bjørk) | | | | | | | | | | | | | | | | |
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| **Herbaceauos plants** | | | | | | | | | | | | | | | | |
| Solidago virgaurea (gullris) | | | | | | | | | | | | | | | | |
| Potentilla erecta (tepperot) | | | | | | | | | | | | | | | | |
| Trientalis europaea (skogsjerne) | | | | | | | | | | | | | | | | |
| Lycopodium annotinum (stri kråkefot) | | | | | | | | | | | | | | | | |
| Polygonum viviparum (harerug) | | | | | | | | | | | | | | | | |
| Cornus suecica (skrubbær) | | | | | | | | | | | | | | | | |
| Maiblom (Maianthemum bifolium) | | | | | | | | | | | | | | | | |
| Anemone nemorosa (hvitveis) | | | | | | | | | | | | | | | | |
| Oxalis acetosella (gaukesyre) | | | | | | | | | | | | | | | | |
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| **Graminoids** | | | | | | | | | | | | | | | | |
| Avenella flexuosa (smyle) | | | | | | | | | | | | | | | | |
| Anthoxanthum odoratum (gulaks) | | | | | | | | | | | | | | | | |
| Molinia caerulea (blåtopp) | | | | | | | | | | | | | | | | |
| Luzula pilosa (hårfrytle) | | | | | | | | | | | | | | | | |
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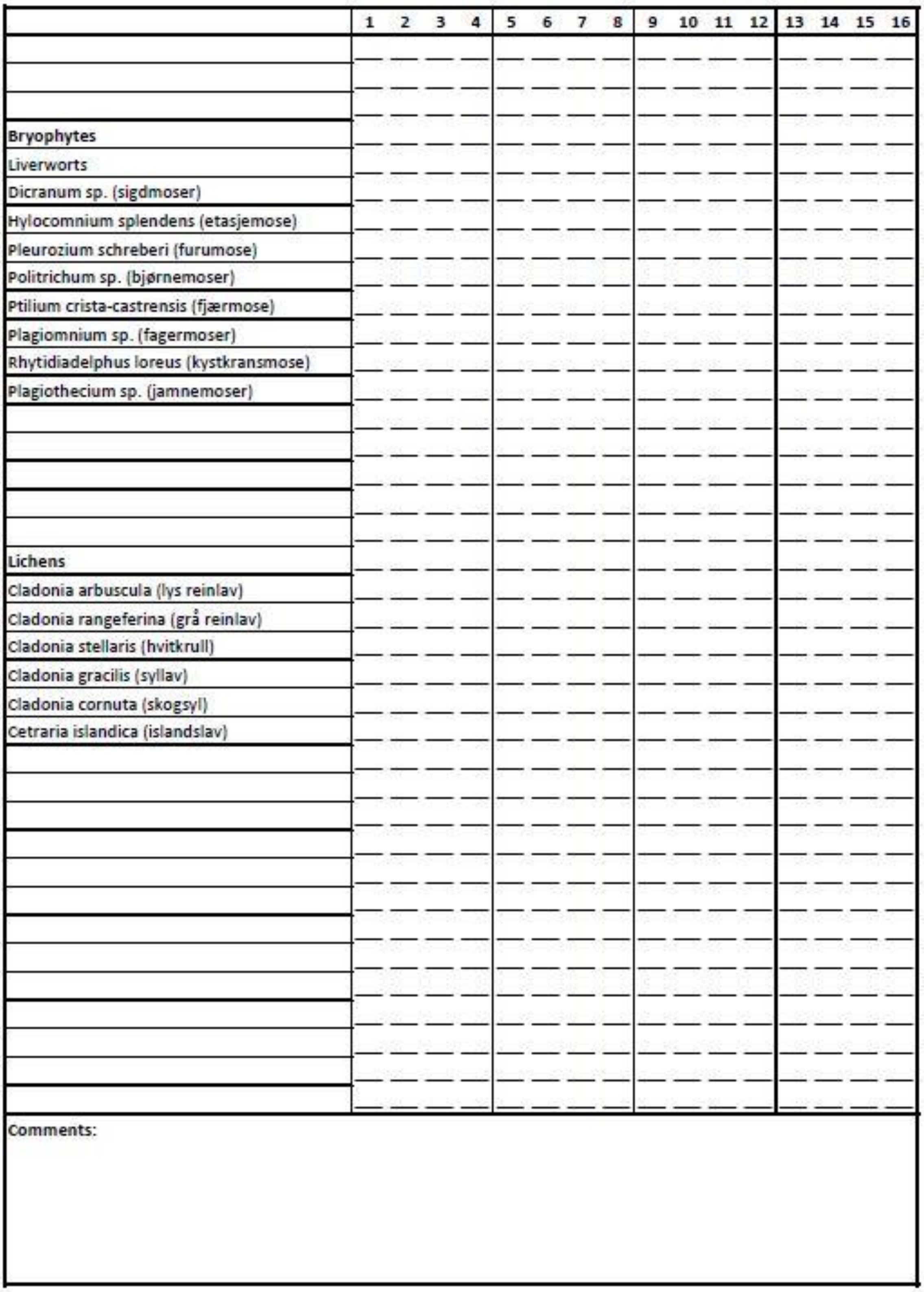

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| **Bryophytes** | | | | | | | | | | | | | | | | |
| Liverworts | | | | | | | | | | | | | | | | |
| Dicranum sp. (sigdmoser) | | | | | | | | | | | | | | | | |
| Hylocomnium splendens (etasjemose) | | | | | | | | | | | | | | | | |
| Pleurozium schreberi (furumose) | | | | | | | | | | | | | | | | |
| Politrichum sp. (bjørnemoser) | | | | | | | | | | | | | | | | |
| Ptilium crista-castrensis (fjærmose) | | | | | | | | | | | | | | | | |
| Plagiomnium sp. (fagermoser) | | | | | | | | | | | | | | | | |
| Rhytidiadelphus loreus (kystkransmose) | | | | | | | | | | | | | | | | |
| Plagiothecium sp. (jamnemoser) | | | | | | | | | | | | | | | | |
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| **Lichens** | | | | | | | | | | | | | | | | |
| Cladonia arbuscula (lys reinlav) | | | | | | | | | | | | | | | | |
| Cladonia rangeferina (grå reinlav) | | | | | | | | | | | | | | | | |
| Cladonia stellaris (hvitkrull) | | | | | | | | | | | | | | | | |
| Cladonia gracilis (syllav) | | | | | | | | | | | | | | | | |
| Cladonia cornuta (skogsyl) | | | | | | | | | | | | | | | | |
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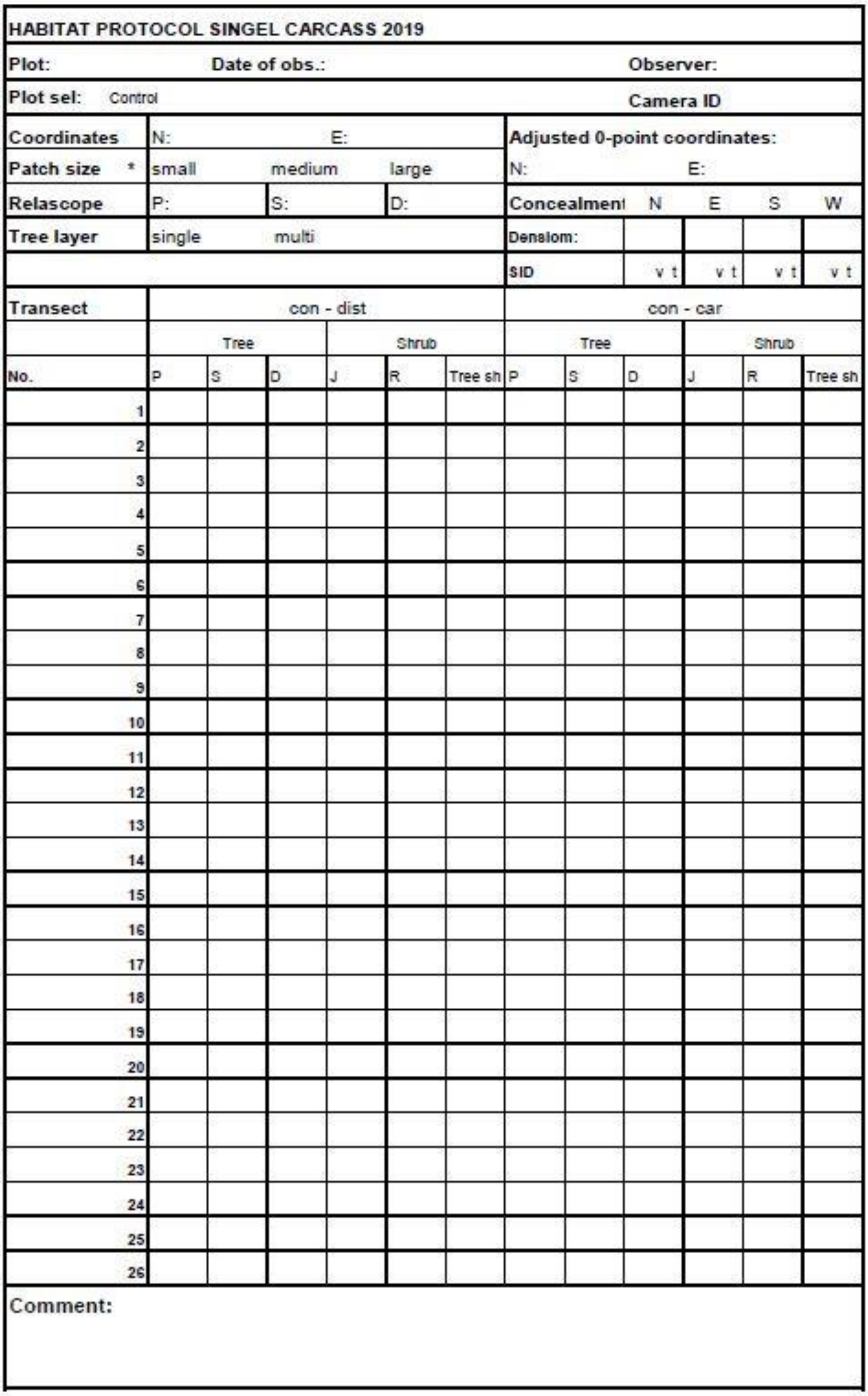
**Comments:**

*Figure S1:* Plot protocol single carcass, a form that was used in the field to analyse the vegetation at every single plot, one form per treatment type. In the form we registered the different cover at the ground (stone, soil, plant, bryophyte, lichen, carcass and litter), the microtopography, and we registered presence of all plant species.



**HABITAT PROTOCOL SINGEL CARCASS 2019**

**Plot:** **Date of obs.:** **Observer:**

**Plot sel:** Control **Camera ID**

**Coordinates** N: E:

**Patch size** * small medium large

**Relascope** P: S: D:

**Tree layer** single multi

**Adjusted 0-point coordinates:**

N: E:

| **Concealment** | N | E | S | W |
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| **Transect** | con - dist | | | | | | con - car | | | | | |
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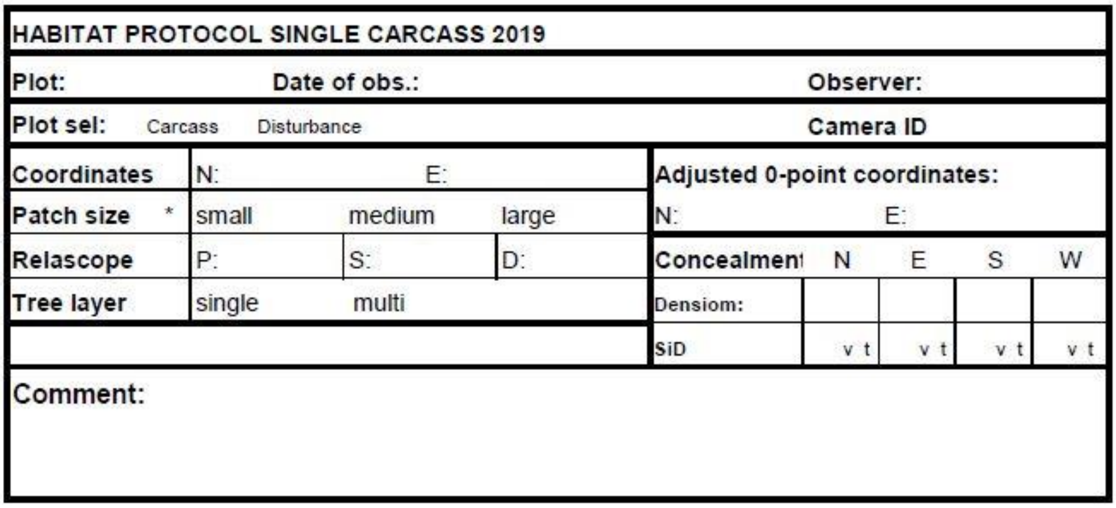
**Comment:**



**HABITAT PROTOCOL SINGLE CARCASS 2019**

**Plot:** **Date of obs.:** **Observer:**

**Plot sel:** Carcass Disturbance **Camera ID**

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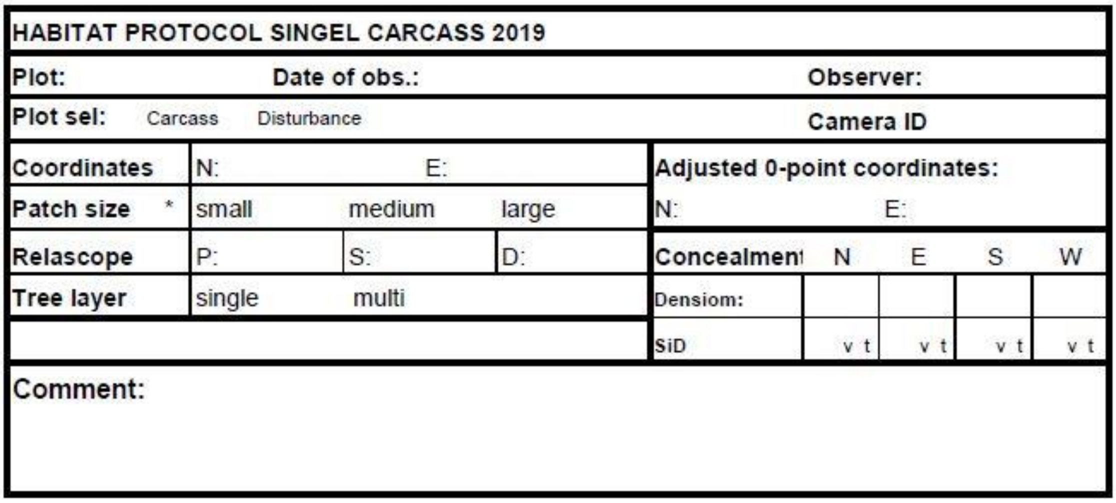
| **Coordinates** | N: | E: | | **Adjusted 0-point coordinates:** | | | | |
| **Patch size** * | small | medium | large | N: | E: | | | |
| **Relascope** | P: | S: | D: | **Concealmen** | N | E | S | W |
| **Tree layer** | single | multi | | **Densiom:** | | | | |
| | | | | **SiD** | v t | v t | v t | v t |

**Comment:**



**HABITAT PROTOCOL SINGEL CARCASS 2019**

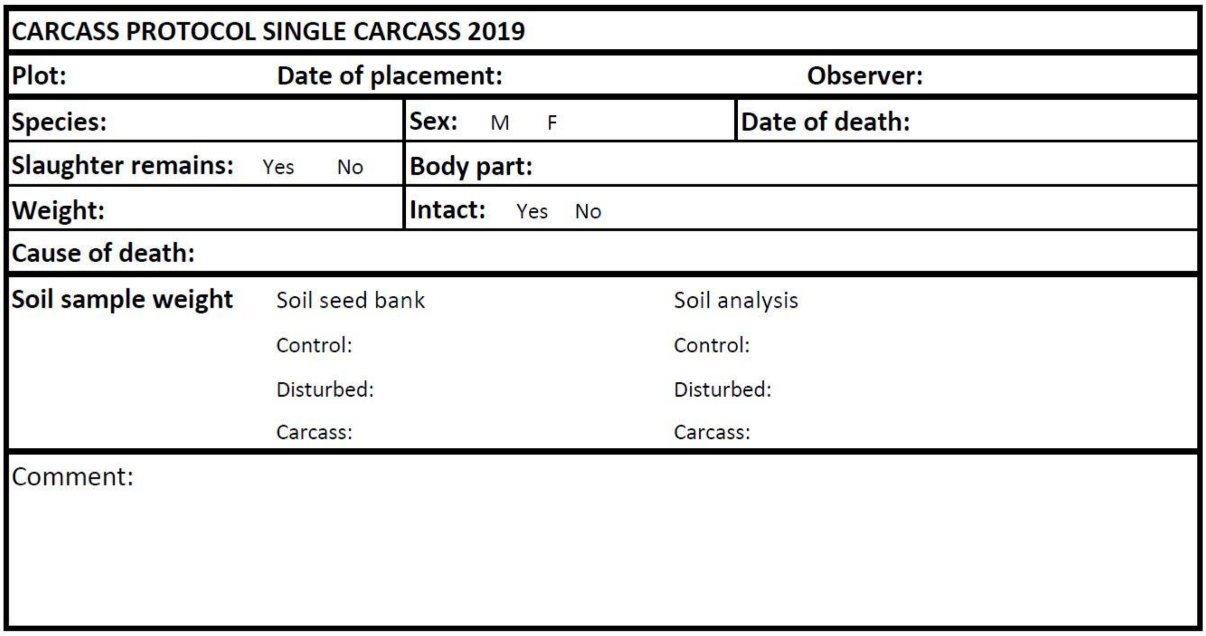
**Plot:** **Date of obs.:** **Observer:**

**Plot sel:** Carcass Disturbance **Camera ID**

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Coordinates** | N: | E: | | **Adjusted 0-point coordinates:** | | | | |
| **Patch size** * | small | medium | large | N: | E: | | | |
| **Relascope** | P: | S: | D: | **Concealmen** | N | E | S | W |
| **Tree layer** | single | multi | | **Densiom:** | | | | |
| | | | | **SiD** | v t | v t | v t | v t |

**Comment:**

*Figure S2:* Habitat protocol single carcass was used in the field to analyse the vegetation at every single plot, one form per treatment type. It was registered the patch size, trees where counted in a Relascope (pine, spruce and deciduous), tree layer, canopy with a densiometer and the plot visibility (in all directions of heaven and if it were vegetation or terrain that stopped the visibility). Exclusively for the control plot was a transect registration.



**CARCASS PROTOCOL SINGLE CARCASS 2019**

**Plot:** **Date of placement:** **Observer:**

**Species:** **Sex:** M F **Date of death:**

**Slaughter remains:** Yes No **Body part:**

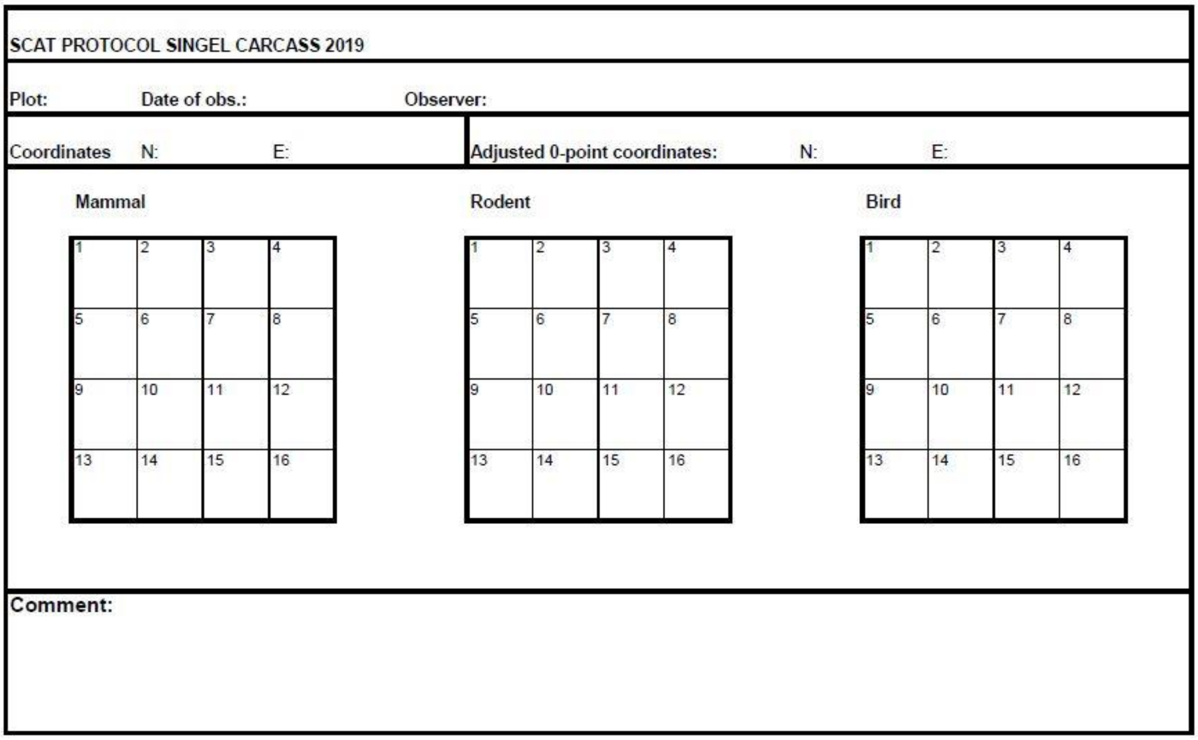
**Weight:** **Intact:** Yes No

**Cause of death:**

| | | |
|---|---|---|
| **Soil sample weight** | Soil seed bank | Soil analysis |
| | Control: | Control: |
| | Disturbed: | Disturbed: |
| | Carcass: | Carcass: |

Comment:

*Figure S3:* Carcass Protocol single carcass. The field form that was used the second time the plots were visited, when the carcasses were deployed. In the form we registered information about the carcass in addition to information about the soil samples we took.



SCAT PROTOCOL SINGEL CARCASS 2019

Plot: Date of obs.: Observer:

Coordinates N: E: Adjusted 0-point coordinates: N: E:

Mammal

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| 5 | 6 | 7 | 8 |
| 9 | 10 | 11 | 12 |
| 13 | 14 | 15 | 16 |

Rodent

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| 5 | 6 | 7 | 8 |
| 9 | 10 | 11 | 12 |
| 13 | 14 | 15 | 16 |

Bird

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| 5 | 6 | 7 | 8 |
| 9 | 10 | 11 | 12 |
| 13 | 14 | 15 | 16 |

Comment:

*Figure S4:* Scat protocol single carcass was used the third time the plots where visited. The field form registered the number of scats that was found at the plots. The scats were sorted between mammal, rodent and bird scats.

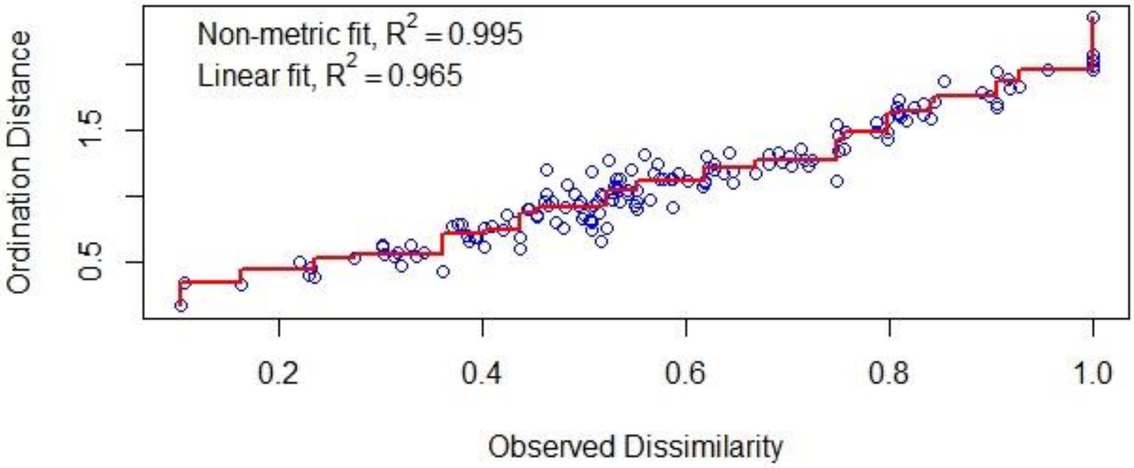


*Figure S5:* The stressplot shows a good validation with a small ordination distance of the observed dissimilarities regarding the ordination plot in figure 4.

*Table S1*: Shows an overview of which functional groups the different species are categorized in.

| **Funtional group** | **Species** |
|---|---|
| Cervidae | Moose (Alces alces), red deer (Cervus elaphus), roe deer (Capreolus capreolus), reindeer (Rangifer tarandus) |
| Rodentia | Mountain hare (*Lepus timidus*), Eurasian red squirrel (*Sciurus vulgaris*) |
| Carnivora | Red fox (*Vulpes vulpes*), European pine marten (*Martes martes*), European badger (*Meles meles*), stoat (*Mustela erminea*) |
| Accipitridae | Golden eagle (*Aquila chrysaetos*), northern goshawk (*Accipiter gentilis*), Eurasian sparrowhawk (*Accipiter nisus*), rough-legged buzzard (*Buteo lagopus*), |
| Corvidae | Common raven (*Corvus corax*), hooded crow (*Corvus cornix*), Eurasian magpie (*Pica pica*), Eurasian jay (*Garrulus glandarius*), Siberian Jay (*Perisoreus infaustus*) |
| Tetraonini | Western capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*), hazel grouse (*Tetrastes bonasia*) |
| OtherBirds | Thrush (*Turdidae*), passerine (*Passeriformes*)woodpecker (*Piciformes*), sandpipers (*Scolopacidae*) |

*Table S2:* The table shows an overview of over the different variables collected in the field work, and an explanation.

| **Variable** | **Explanation** |
|---|---|
| PlotNr | Identification number of the plots. |
| Type | Treatment type, control plot, carcass plot, and disturbed plot. |
| CameraID | Identification number of the camera trap. |
| CameraDays | Number of days with the carcass activated. |
| CarcassDays | Number of days with the carcass present at the plot. |
| CarcassProportion | Proportion between days with carcass present and number of camera days. |
| VacciniumDispersers | Potential dispersers of *Vaccinium spp*. |
| StoneCover | Estimated percent of plot covered of stones. |
| SoilCover | Estimated percent of plot covered of soil. |
| PlantCover | Estimated percent of plot covered of plants. |
| BryophyteCover | Estimated percent of plot covered of bryophytes. |
| LichenCover | Estimated percent of plot covered of lichens. |
| CarcassCover | Estimated percent of plot covered of carcass. |
| LitterCover | Estimated percent of plot covered of litter. |
| Microtopography | Average length of microtopography at ground level (six length measured). |
| PatchSize | Size of the patch (with relative similar vegetation and terrain) the plots are placed in. Small, medium and large. |
| Pine | Number of scots pine (*Pinus sylvestris*) counted in a relascope at the plot. |
| Spruce | Number of Norway spruce (*Picea abies*) counted in a relascope at the plot. |
| Deciduous | Number of deciduous counted in a relascope at the plot. |
| TreeLayer | Estimated tree layer in the patch, multi or single. |
| Densiometer | Average canopy cover measured with a densiometer in all four cardinal directions. |

| | |
|---|---|
| SID | Sight in distance. Average distance in meter a 50 centimetres high orange stick at the plot is visible from all four cardinal directions. |
| PlantDiversity | Number of plant species present inside the 1x1 m2. |
| SpeciesCarcass | Species of the carcass. |
| WeightKG | Weight of the carcass in kilograms. |

*Table S3:* The table shows an overview the wildlife camera trap data. It shows the number of visits from the different functional group in addition to total numbers, the mean, and how long the cameras were active in total and with carcass.

| | **Camera Days** | **Carcass Days** | **Vaccinium Dispersers** | **Vaccinium Dispersers Carcass** | **Vaccinium Dispersers Control** | **Carcass Plot** | **Control Plot** | **Total** |
|---|---|---|---|---|---|---|---|---|
| **#** | 2338 | 998 | 3985 | 3884 | 101 | 4011 | 182 | 4193 |
| **Mean** | 106 | 45 | 181 | 177 | 5 | 182 | 8 | 191 |
| | | | | | | | | |
| | **N Species** | **Cervidae** | **Rodentia** | **Carnivora** | **Accipitridae** | **Corvidae** | **Tetrao-nini** | **Other Birds** |
| **#** | 27 | 91 | 27 | 344 | 53 | 3351 | 23 | 304 |
| **Mean** | NA | 4 | 1 | 16 | 2 | 152 | 1 | 14 |