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Predation-induced ungulate carcasses mediate vegetation composition in the boreal ecosystem

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ABSTRACT

Apex carnivores are mostly recognized for their effects on ecosystem processes through altering population dynamics and behaviour of their prey. Apex carnivores may also affect lower trophic levels through the distribution of ungulate carcasses. Such direct effects of predation on lower trophic levels are, however, poorly understood. Ungulate carcasses typically disturb soil and vegetation locally and enrich the soil with nutrients, which affect composition of the vegetation. In this study, I assessed vegetation composition in relation to carcasses of wolf-killed (*Canis lupus*) moose (*Alces alces*) in the boreal forest in southcentral Sweden. I compared composition of vascular plants, bryophytes and lichens at 12 carcass sites, each one paired with a nearby (25-50m) control site without carcass. I recorded the abundance of all species within nine vegetation plots at each carcass and control site, with one plot placed at the kill spot. Using generalized linear mixed models, I found that the carcasses created intense local disturbances and reduced both field (vascular plants) and ground cover (bryophytes and lichens), with the most dramatic effect in the centre of the carcass plot. Carcasses presence accounted for 11% of the explained variation in the species composition, although the effects were very local. Results from a detrended correspondence analysis revealed that forest age was the most important gradient in explaining patterns in species composition. Disturbance from carcasses was the second most important. I used indicator value analysis to identify winners and losers of carcass presence, and found that seedlings of *Betula pubescens/pendual* and *Pinus sylvestris* were more abundant on the carcass centre plots than elsewhere. Additionally, three mosses were positively affected by carcass disturbance (*Pohlia nutans*, *Bryum sp*., *Plagiomnium ellipticum*), and one lichen (*Cladonia arbuscula*) was identified as a loser. The disturbance from carcasses showed several similarities with uprooting of trees, as it releases competitive interactions and makes space available for species regenerating from the diaspore bank. Because uprooting's are rare in the heavily managed forest, this may increase the importance of carcasses as disturbances in the boreal forest. My results emphasize that apex predators can have important ecological roles other than numeric and trait mediated cascading effects, as predation events create local biogeochemical hotspots. This highlight the importance of conservation of apex predators in the ecosystem to keep ecosystem functioning intact.

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INTRODUCTION

Apex carnivores affect ecosystems directly and indirectly, through their effects on the demography and behaviour of their prey (Creel & Christianson 2008; Peterson et al. 2003; Ripple & Beschta 2003; Ripple & Beschta 2012a). In recent time, predation-induced trophic cascades have been increasingly recognised as important mechanisms in ecosystem functioning (Orrock et al. 2010; Ripple & Beschta 2012b; Schmitz et al. 2004; Smith et al. 2003). A famous case is the reintroduction of grey wolves (*Canis lupus*) in Yellowstone National Park in 1995-1996, after 70 years of wolf absence. Synergic with climate and human harvest (Eberhardt et al. 2007; Vucetich et al. 2005), wolf predation has influenced the abundance and distribution of elk (*Cervus canadensis*) through direct effects on elk mortality and indirect effects on elk behaviour (Ripple & Beschta 2004). After the wolf reintroduction, ungulates avoided riparian areas, their previously preferred habitat, and the reduction in herbivory led to an increase in riparian vegetation (Beschta & Ripple 2012). In turn, this resulted in an increase in available habitat for bird populations and beavers (*Castor canadensis*) (Ripple & Beschta 2012b) Another way top-level carnivores may affect the ecosystem is through the distribution of carcasses. Carcasses are local disturbances with a physical (e.g. compression of vegetation), chemical (e.g. corporal fluids), and biological (e.g. external microbiota) components, which affect soil biogeochemistry, and can propagate further into the food web (Figure 1).

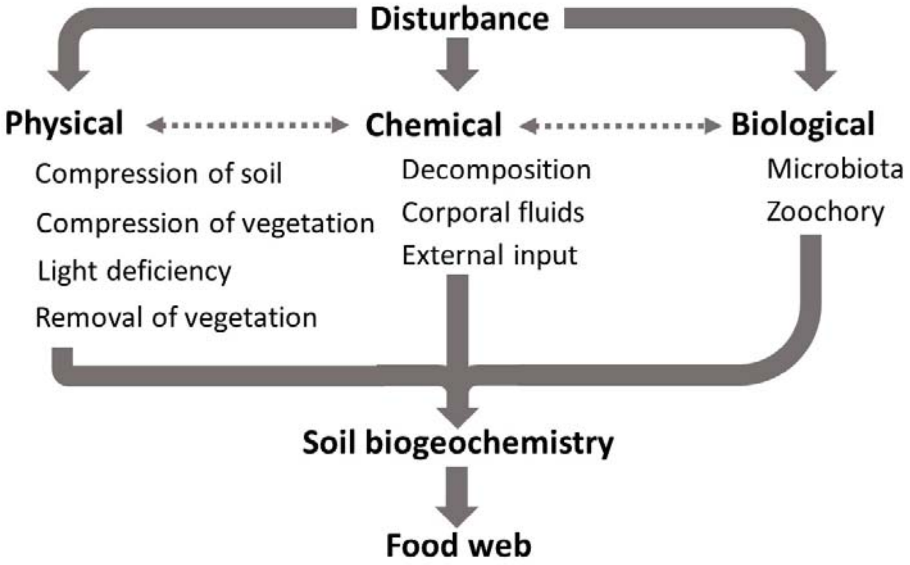

Figure 1 *Conceptual diagram of the different disturbance effects a carcass may have on the soil biochemistry: physically: through compression and removal of vegetation; chemical: through the decomposition of cadaveric material; biologically: through alteration of soil microbiota and addition of seeds through zoochory, which all may propagate further into the food web.*

Carcasses may physically disturb the ground by covering up the vegetation beneath and kill it by blocking for the light (Towne 2000). The chemical component is determined by two factors: temperature and predation/scavenger activity. First, the temperature determines how fast the carcasses is decomposed (DeVault et al. 2003). When the ambient temperature is high, arthropod, bacterial, and fungal growth is increased and the decomposition rate is increased (Carter et al. 2007). Under colder conditions, the rate of decomposition is much slower, and a larger portion of the carcass becomes available for predators and scavengers. This determines whether the nutrients are recycled locally, or transferred into surrounding areas via predator/scavenger movements. If most nutrients are recycled locally, carcasses may release huge amounts of nitrogen as well as other macronutrients, that can create biochemical hotspots (Barton et al. 2013b; Bump et al. 2009a; Melis et al. 2007). Increased levels of soil nutrients may propagate further into the food web and affect the productivity (Bruun et al. 2005; Danell et al. 2002; Gharajehdaghipour et al. 2016) or the composition of the vegetation (Barton et al. 2016; Towne 2000). The biological component of the disturbance is seed dispersal and microbiota. Scavengers, like brown bears (*Ursus arctos*) may physically disturb the soil, but may also disperse seeds. Recent studies have examined the effects of carcases on soil heterogeneity (Danell et al. 2002) and vegetation (Barton et al. 2013b; Barton et al. 2016; Towne 2000), but few have studied have linked prey remains to biochemistry (Bump et al. 2009a; Melis et al. 2007) and vegetation (Bump et al. 2009b).

Carcass effects seem to be most pronounced where the contrasts are large, e.g. a large amounts of carcass biomass introduces nutrients into a poor environment. Studies from the tundra showed a pronounced effect of carcasses on both soil nutrients and vegetation productivity (Danell et al. 2002; Towne 2000). In contrast, no strong effect on the vegetation was found in the nutrient rich temperate forest of Bialoweiza (Melis et al. 2007). In the boreal forest, which is nitrogen limited (Bonan & Shugart 1989), large carnivore predation on ungulates may be an important source of disturbance that leads to increased local soil nutrients, and soil and vegetation heterogeneity. Even highly consumed and scavenged carcasses have shown to affect soil nutrients (Bump et al. 2009a; Melis et al. 2007) and the vegetation (Bump et al. 2009b). Carcasses are often a hotspot of large carnivore and scavenger activity, receiving additional organic and inorganic material from faeces and/or hair or feathers from scavengers (Wilson 2003, Carter et al. 2007). In addition, if plant growth is enhanced, the soil can be further amended with fecal matters from grazers (Turner et al. 2014).

Vascular plants, bryophytes and lichens may respond differently to disturbance, due to their life-history attributes (Bruun et al. 2005; Jonsson & Esseen 1998). Vascular plants take up nutrients through their roots and can benefit from increased levels of nutrients in the soil, even though the response depends on species or growth form (Bruun et al. 2005; Grime 2006; Shaver & Chapin 1980). Bryophytes and lichens acquire nutrients and water through the surface of their bodies, but may still be able to utilize increased levels of soil nutrients (Ayres et al. 2006; Rousk et al. 2013). Another important factor determining an organism's response to a disturbance is the temporal and spatial extent of the disturbance (Jonsson & Esseen 1998; Rydgren et al. 2004). In the boreal forest, most vascular plants regenerate from roots or shoots (e.g. *Vaccinium spp.*, *Calluna vulagaris*) (Rydgren et al. 2004) while only a few regenerates from the diaspore bank (*Melampyrum pratense*, *Betula spp.*)(Jonsson & Esseen 1998). For comparison, bryophytes have a large variety of regeneration methods, that may make them fast colonizers (Jonsson & Esseen 1998). Species like *Hylocomium splendens* and *Pleurozium schreberi* most commonly establish from detached shoot fragments (Jonsson 1993). Many other species of bryophytes regenerate from asexual or sexual propagules, present in the soil propagule bank (Rydgren & Hestmark 1997).

The large carnivore guild in the boreal forest of Fennoscandia includes wolves (*Canis lupus*), brown bears, wolverines (*Gulo gulo*), and lynx (*Lynx lynx*). Moose is the staple prey of wolves in Scandinavia and bears are both efficient predators of neonate ungulates and scavengers on wolves' prey (Tallian et al. 2017). Moose is the most important prey species for wolfs and predation rates has been found to be 0.60 prey animal/group per day (Sand et al. 2008). In addition, estimated bear kills of moose calves is estimated to somewhere between 6.1 and 9.4 every year (Swenson et al. 2007). As predation is not random, prey distribution by apex carnivores may modulate heterogeneity in soil nutrient (Bump et al. 2009a), which may affect the composition of the vegetation. No studies currently exist on the role of carcasses of large carnivore prey to mediate soil and vegetation heterogeneity in the boreal forest ecosystem, and no study elsewhere explicitly linked predation events to the vegetation community (vascular plants, bryophytes, lichens) in its entirety. Therefore, the overall aim of this study is to assess the effect of wolf-killed moose carcasses on the cover and composition of the vegetation of vascular plants, bryophytes and lichens. I hypothesized (H1) that carcasses create local disturbances to both field and ground cover and predicted that cover would be lower at carcass sites compared to control sites, and that cover would increase with increasing distance from the carcass centre. Second, I hypothesize (H2) that carcasses affect the entire vegetation community and predict that carcass presence and related disturbance is among the most explanatory factors to explain variation in the composition of vascular plants, bryophytes, and lichens. In addition, I hypothesize (H3) that carcasses generate trued winners and losers in species and growth forms in terms of abundance. I predict, in accordance with the literature, that tree winners will include tree seedlings, and losers will be dominated by shrubs and lichens. The specific questions that I pose in this thesis are: How do moose carcasses affect the vegetation composition (RQ1)? Are some plant species or growth forms favoured by carcasses (RQ2)? Is there a gradient in species composition / soil nutrients with increasing distance from the centre of the carcass plots?

METHODS

Study area

The study was conducted in south-central Sweden and covers the western part of Gävleborg county, central parts of Dalarna county, and southern Jämtland county (Figure 2). The area is hilly, with elevations ranging from 200 to 700 meters and covers around 13.000 km^2 (Swenson et al. 1999). Human settlement occurs throughout the study area as small, scattered villages and human population density was 4-7 habitants/km2 in 2011 (Ordiz et al. 2014). Throughout the landscape there is a dense network of gravel roads (1 ± 0.5 km/km2 –mean and SD–, range 0–4.6 km/km2) (Ordiz et al. 2014). The area mostly comprises of highly managed boreal coniferous forest (~ 80 %) with 90-100 year harvest turnover rate. Intensive forestry resulted in a mosaic of small patches of differently aged cohorts, with a median patch size of 22.500 m^2 (mean: 80.600 m^2) (Moe et al. 2007). The rest of the area was comprised mostly of bogs and lakes (Swenson et al. 1999). The climate is relatively cold and moist and the temperature ranges from an average of -7° C in January to an average of 15° C in July. Snow cover typically lasts from late October until early May, usually around 160-170 days (Swenson et al. 1999).

The vegetation is poor in species richness, with relatively few species dominating the area. The most common tree species are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Dahle & Swenson 2003). Other common tree species include common birch (*Betula pubescens*) and silver birch (*Betula pendula*). The shrub layer comprises mostly of juniper (*Juniperus communis*), willow species (*Salix* spp.), and rowan (*Sorbus acuparia*). The field layer is dominated by bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idea*), crowberry (*Empetrum* spp.), and heather (*Calluna vulgaris*). The moss community mainly consists of red-stemmed feathermoss (*Pleurozium shreberi*), glittering woodmoss (*Hylocomium splendens*) and forkmosses (*Dicranum* spp.). The lichen community is comprised mostly of cup-lichens (*Cladonia* spp.).

The brown bears, wolves, lynx, and wolverine make up the community of large carnivores and the red fox (*Vulpes vulpes*), badger (*Meles meles*), pine marten (*Martes martes*) and a variety of birds, including the raven (*Corvus corax*), are the most important members of the nonpredatory, scavenging community.

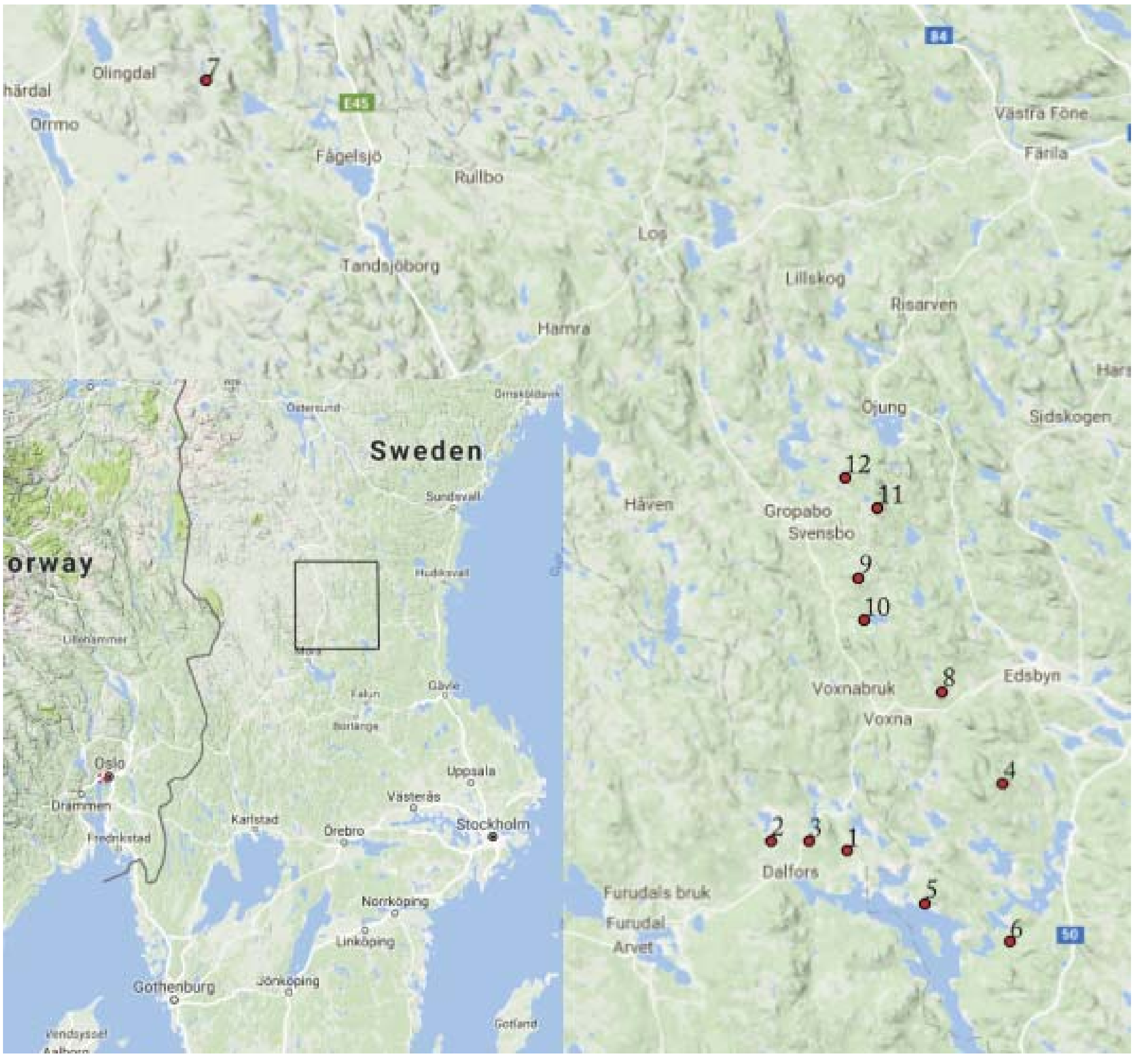

Figure 2 *The study area is located in south-central Sweden, with the 12 different locations. Description of the locations can be found in Table 1.*

The moose population has an estimated winter population density of 500 individuals per 1000 km^2 (Rauset et al. 2012), and roe deer are present in lower numbers. The bear population reaches densities of 30 individuals per 1000 km^2 (Bellemain et al. 2005), and the number of wolf packs in the area varies from year to year after the recolonization of the area about 10 years ago. Two wolf packs were present in the area during our study period: the Kukumaki and Tandsjön packs. In 2014, both packs reproduced and had at least four members (Svensson et al. 2015). Early in 2015 the Tandsjön pack was killed as a management measure, but a marking pair, the first step in the formation of a new wolf pack, was later detected in the same area (Wabakken et al. 2016).

Data collection

The Scandinavian wolf project (SKANDULV) and the Scandinavian Brown Bear Research Project (SBBRP) recorded freshly killed wolf and kills in winter and spring between 2011 and 2016 in the study area, as part of wolf predation and bear-wolf interactions studies (Tallian et al. 2017). From that database, we selected carcasses of adult (≥1 year old) moose that were confirmed as wolf kills by the field crew. For this thesis, we selected carcasses that originated from spring (2014 and 2015) and at locations without snow cover when the carcass was found. We validated the carcass locations in the field in May 2016 and only selected locations for which we could verify the exact carcass centre using pictures from previous fieldwork and where we could find physical evidence of a carcass (e.g., pieces of bone or hair tufts). We marked each carcass centre with a stick and a new GPS position for later fieldwork (Figure 3). For all except one carcass, SKANDULV and SBBRP had installed camera traps to monitor the use of the kills by wolves, bears, and the rest of the scavenger community. At some of the locations, the carcass had been dragged from the original kill spot, which may have influenced the degree of disturbance at these locations.

I compared vegetation composition between sites with moose carcasses and a nearby control without a carcass. Control sites were selected in the same patch of habitat type where the carcass was, and at the same distance to the edge of the habitat patch type, slope steepness and orientation. Control sites were between 25 and 50 meters from the carcass site. Habitat types were defined according to the Swedish Forest Inventory System (Karlsson & Westman 1991). To control for additional environmental variation, I measured on each plot the canopy cover with a densiometer and the microtopography of the plot with the chain method (Rydgren et al. 2013). I measured stem density with a relascope for each location at both carcass and control. Elevation, slope and aspect for each site was later extracted from digital maps. Soil depth, soil macronutrients and pH were measured by a colleague master student in a parallel project.

Figure 3 *Pictures taken during carcass validation in May 2016.* ***a:*** *Location number 12, carcass from 2014, only red fox detected on camera,* ***b:*** *Location number 10, carcass from 2014, raven and red fox detected on camera,* ***c:*** *Location number 9, carcass from 2015, marten, red fox, wolverine and brown bear detected on camera,* ***d:*** *Location number 11, carcass from 2014, nothing detected on camera,* ***e:*** *Location number 1, carcass from 2015, bear detected on camera,* ***f:*** *Location number 8, carcass from 2015, brown bear detected on camera, one month after the death of the animal. Photo: Marte Olsen*

To obtain a representative sample of the vegetation, I stratified survey plots (0.5*0.5m) within a 5m radius around the carcass and the control site centres, respectively (Figure 4). I divided each circle into four quadrants and I placed one survey plot at the centre of each site. I distributed two plots per quadrant, according to a randomly selected distance and a randomly selected direction. All plots had to be at least 1m apart, and new random distances and directions were drawn until this criterion was met. We marked each plot and avoided trampling or other disturbances on the plots.

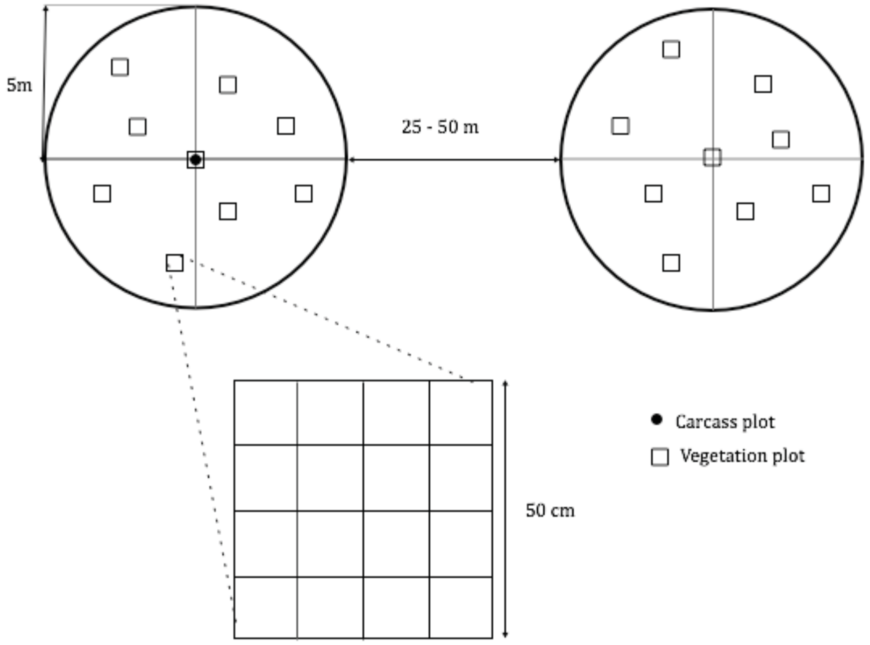

Figure 4 *Schematic representation of the sampling design at carcass and control sites. One plot was always placed on the centre of the carcass and control. Two vegetation plots were placed randomly in every quadrant. The frequency of vascular plants, bryophytes and lichens were sampled as the frequency in 16 subplots.*

I surveyed vegetation at carcass and control sites in August and September 2016. I recorded the frequency of vascular plants, bryophytes and lichens as frequency of 16 subplots (Figure 4) within each survey plot (Rydgren et al. 2004; Rydgren et al. 2013). Species that could not be identified in the field were collected for later identification in the lab. Total vegetation cover was estimated in percent as field- and ground cover. In addition, I estimated cover for each species separately.

I followed the vegetation nomenclature according to the Norwegian Biodiversity Information Centre (www.artsdatabanken.no). For some taxa, e.g. for moss, liverworts and lichens, I chose to use genus as the highest taxonomic level, because of the time it would have taken to identify at the speciesism to the species level, i.e. *Bryum*, *Scurio-hypnum, Sphagnum* and *Splachnum* for mosses, *Calypogeia* and *Cephalozia* for liverworts, and *Cladonia* for lichens).

Data analysis

Field and ground cover

To test whether the ground- and field cover differed between carcass and control sites, I used general linear mixed effect models using the ‘lme4’ in R (Bates et al. 2014) for binomial proportion data. I used the vegetation cover estimate as a response variable, I considered carcass/control, canopy cover (scale 0 – 96, where 0 is complete cover), microtopography (cm), year, distance from the centre of the plot (m) and the interaction between distance and carcass/control as potentially explanatory variables. I included location as a random effect on the intercept. I ran all possible model combinations of explanatory variables using the MuMIn package (Barton 2013), and for model selection I considered the simplest model with the lowest AICc (in a range of 2) as the most parsimonious model of all candidates (Arnold 2010; Burnham & Anderson 2003).

Species composition

I used ordination methods to examine the main gradients in species composition. I ran a Detrended Correspondence Analysis (DCA) with the ‘decorana’ function in the vegan package 2.4.1 (Oksanen et al. 2013) and with default settings. Running and evaluating DCA and GNMDS concurrently has been recommended to assess the robustness of the results (Pers comm, Rune Halvorsen). I used τ to evaluate correlations between the GNMDS and the DCA, and high correlations between the axes of the different methods suggest that results are robust. Complementary with the DCA, I ran Global Non-Metric Multidimensional Scaling (GNMDS) with the ′metaMDS′ function in the vegan package 2.4.1 (Oksanen et al. 2013) based on a Bray-Curtis dissimilarity index. I specified the random starting configurations to 200, and maximum number of iterations to 999 (Rydgren et al. 2013). I obtained two-, three- and four-dimensional solutions for the GNMDS. I used Kendall´s rank correlation coefficients (τ) to validate the number of dimensions (Kendall 1938).

Furthermore, I added environmental variables to the ordination through the ‘envfit’ function in the vegan package. The variables included were soil nutrients (site level: phosphorus (mg/100mg soil), calcium (mg/100mg soil), magnesium (mg/100mg soil), potassium (mg/100mg soil); plot level: nitrogen (%), carbon (%), C:N ratio), soil depth (cm) (plot level; substrate (cm), mineral (cm) and total depth (cm)), cover (%) (field- and ground cover), soil pH (ordinal scale 1-14), microtopography (cm), canopy cover, elevation (m), slope (degrees), and distance to the centre of the plot (m). All soil data was collected and analysed in a parallel project. All the numeric variables were zero-skewness transformed (Pers comm, Rune Halvorsen). I used default settings, but specified the number of permutations to 999.

To explicitly test whether species composition differed between carcass and control sites, I used Partial Constrained Correspondence Analysis (PCCA) in the vegan package. I always considered ‘Site’ (locations) as a conditioning variable due to the large variation in habitats across the locations. The PCCA was performed through the function ´permutest´ in the vegan package (Oksanen et al. 2013). I used the species composition matrix as the response variable, carcass/control as a constraining variable and site as a conditioning variable. I used default settings, but specified number of permutations again to 999. I chose to use Linear Combination plot scores (LC) instead of Weighted Average (WA) plot scores, since the use of WA scores has little meaning (Pers. comm, Rune Halvorsen).

Indicator species

To examine if any species or genus of vascular plants, bryophytes or lichens preferred or avoided carcass sites, I used the ´indicspecies´ package (De Caceres et al. 2016) and the function ´multipatt´. The function measures the association between a species and a group (e.g. habitat type, disturbance severity, carcass/control) through an indicator value analysis (Cáceres et al. 2012). The indicator value is composed by both relative abundance and relative frequency. The relative abundance is the mean abundance in plots within the group over the mean abundance in all plots. The relative frequency is the number of subplot frequencies within the group over the total number of subplot frequencies. I decided to divide the data into three groups: carcass-centre plots, carcass plots and control plots and then described the statistical significance of the relationship with a permutation test. I specified the number of permutations to 999, otherwise I used default settings and a threshold level for statistical significance of 0.05. In addition, I tested the association between growth forms (graminoids, dwarf shrubs, herbs, tree seedlings, bryophyte and lichens) and groups using the same specifications.

Variation partitioning

I used variation partitioning by PCCA to find out the effect of three groups of explanatory variables on the variation in species composition (Økland 1999; Rune Halvorsen & Wilson 2003). Each constrained ordination axis has an eigenvalue, which can be interpreted as the relative amount of variation explained by this axis. The sum of eigenvalues on all axis can be seen as a measure of the total variation (total inertia: TI) in species composition in relation to the set of explanatory variables

(Økland 1999). Further, the proportion of the eigenvalue of the selected axes to the total inertia can be seen as the fraction of explained variation caused by this group of explanatory variables (Økland 1999).

I decided to use three sets of variables. In the habitat group, I included: canopy cover, elevation, slope, aspect (8 nominal classes), and forest type (6 classes). In the soil group, I included phosphorus, calcium, magnesium, potassium, carbon, nitrogen, C:N ratio, pH, soil depth, mineral soil depth and substrate soil depth. In the carcass group, I included carcass/control and distance to the centre of the plot. I tested all variables for statistical significance (set at $p \leq 0.05$) and removed the ones not contributing to the variation in species composition as this gives a more realistic estimate of the variation explained (Borcard et al. 1992). I used the ´permutest´ function in vegan to assess the significance. The total number of unique combinations when using three groups are ($2^3 - 1$) (Rune Halvorsen & Wilson 2003). The variation partitioning was carried out by using the PCCA function in the vegan package, with species composition as the response variable, adding all the variables as potentially explanatory variables. I always conditioned for site. First, I calculated the first order partial unions (A, B, C: Figure 5). They are calculated as the variation explained by $G1|(G2 \cup G3)$, $G2|(G1 \cup G3)$, $G3|(G1 \cup G2)$. The second order partial unions (X1, X2, X3; Fig 4) are calculated as $G1 \cap G2|G3$, $G2 \cap G1|G3$ and $G3 \cap G1|G2$, where $\cap$ represents the intersection between those components and their union ($\cup$). Finally, I calculate the third order partial intersections $G1 \cap G2 \cap G3$ (Mathiassen & Halvorsen Økland 2007; Rune Halvorsen & Wilson 2003). I conducted all statistical analyses in R (R Development Core Team 2016)

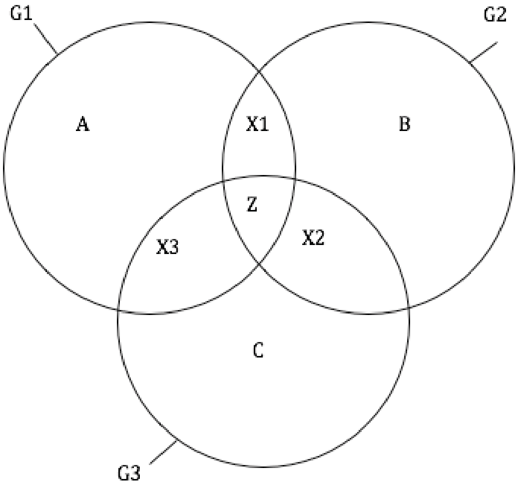

Figure 5 *Venn diagram for partitioning the variation explained by three sets of explanatory variables,* **A:** $G1|(G2 \cup G3)$ **B:** $G2|(G1 \cup G3)$, **C:** $G3|(G1 \cup G2)$, **X1:** $G1 \cap G2|G3$, **X2:** $G2 \cap G1|G3$, **X3**: $G3 \cap G1|G2$, **Z**: $G1 \cap G2 \cap G3$

RESULTS

Carcass selection

In total, I used 13 of the 16 initially selected carcasses for vegetation analysis. Three were left out because of time constraints. These three carcasses originated from 2011 and we could not be sure that we had found the right central carcass spot: First, the exact positions of the GPS points were impossible to find due to GPS error. Second, because of changes in the vegetation (e.g. forestry) it was not possible to identify the position of the carcasses from the cameras. Finally, even though hair and bones were found, we could not be sure if it was dragged here by scavengers or if it was the original carcass site. For statistical analysis, I chose to use 12 of the sites (Table 1). One was left out because it did not satisfy identification requirements. This site had a large amount of grasses and it was impossible to identify the species correctly because of the withering. Of the 12 remaining carcasses, eight were from 2015 and four were from 2014. The Kukumaki wolf pack generated 11 of the carcasses, while only one originated from the Tandsjön pack (Site number 7). I analysed a total of 216 vegetation plots, 108 in carcass plots and 108 in control plots, in four different forest types according to the Swedish Forest Inventory: clearcut (N = 1, tree planting is successful), young forest (N = 5, medium tree is ≥1,3 m but < 10 cm in diameter at breast height), secondary thinning stage (N = 5, medium tree ≥ 10 cm diameter at breast height) and mature forest (N = 1, forest at the age when ca 10 years remain before the final harvest, and older). Note that forest types are subjective classifications of a forest age gradient. We sampled a total of 62 species: 27 vascular plants, a minimum of 31 bryophytes and ≥ 4 lichens. A total of 33 species were found in the centre-carcass plots, 58 different species where found in the carcass plots and 49 in the control plots.

Field and ground cover

The most parsimonious model to evaluate the effect field cover on vascular plants in relation to carcass presence included carcass/control, distance to the centre of the plot, microtopography, and the interaction between carcass/control and distance to the centre as explanatory variables (Table 2). Field cover of vascular plants was significantly higher at control sites compared to carcass sites (Figure 6, Table 3). Field cover of vascular plants remained constant with increasing distance at the control sites, but increased with distance from centre at the carcass sites. Field cover of vascular plant increased with increasing microtopography (Table 3).

Table 1 *The twelve different locations with habitat data and scavenger activity and intensity. % consumed: estimate of the percentage consumed of the carcasses by the SKANDULV team. SFI: Forest type according to Swedish Forest Inventory System (K2: clear-cut, R2: young forest, G1: Secondary thinning, S1: mature forest. Habitat: Description with most common species.*

Nr	**Location**	**% Consumed**	**Year**	**SFI**	**Habitat**	**Scavengers**
1	Myggbo	70 %	2015	K2	Clear-cut	Bear, fox
2	NW Dalfors	99 %	2015	G1	Birch, pine, Vaccinium spp.	No camera
3	NE Dalfors	80 %	2015	R2	Pine, Vaccinium spp.	Fox, raven, wolf
4	Gullbergsbo	50 %	2015	R2	Spruce, Vaccinium spp., herbs and graminoids	Bear, fox
5	Flytåsen	60 %	2015	G1	Pine, Vaccinium spp.	Bear, fox
6	Målångsstuguboderna	90 %	2015	G1	Pine, spruce, Vaccinium spp.	Fox, raven, wolf
7	Färnsjön	99 %	2014	R2	Pine plantation	Wolverine
8	Gräsberget	70 %	2015	G1	Spruce, Vaccinium spp., herbs and graminoids	Bear, fox, raven, marten, wolverine
9	Storberget	90 %	2015	S1	Spruce, Vaccinium spp., herbs and graminoids	Bear, raven
10	Voxnabruk	90 %	2014	G1	Pine, Cladonia spp.	Fox, raven
11	Räkabo	94 %	2014	R2	Pine, birch, spruce.	N/A
12	Mattsmyra	60 %	2014	R2	Pine, Vaccinium spp.	fox

Table 2 *Two best models as ranked according to AIC diagnostics to assess ground and field cover at wolf-killed moose carcasses and paired control sites in the boreal forest of south-central Sweden. Models with ΔAICc scores <2 are shown. I considered the simplest model within this range as the most parsimonious candidate. Additional candidate models are shown in Appendix 1. Df: Degrees of freedom, AIC: Akaike Information Criterion, ΔAIC: Difference in Akaike values between the first and actual model, Weight: Akaike´s weights.*

Model	Df	AIC	ΔAIC	Weight
Fieldcover				
Distance + Microtopography + Type + Distance:Type	7	4779.1	0.00	0.347
Distance + Microtopography + Type + Year + Distance:Type	8	4780.6	1.48	0.166
Ground cover				
Distance + Microtopography + Type + Year + Distance:Type	8	7932.1	0.00	0.636
Distance + Type + Microtopography + Densiometer + Year + Distance:Type	9	7933.9	1.85	0.252

The most parsimonious model to assess ground cover included distance, microtopography, type, year, and the interactions between distance and type as explanatory variables (Table 2). Ground cover of mosses and lichens was significantly higher at control sites compared to carcass sites, and increased with increasing distance to the carcass centre (Figure 7, Table 3). Ground cover of mosses and lichens was negatively related to surface ruggedness. In addition, there was a year effect, with less cover on newer carcass sites.

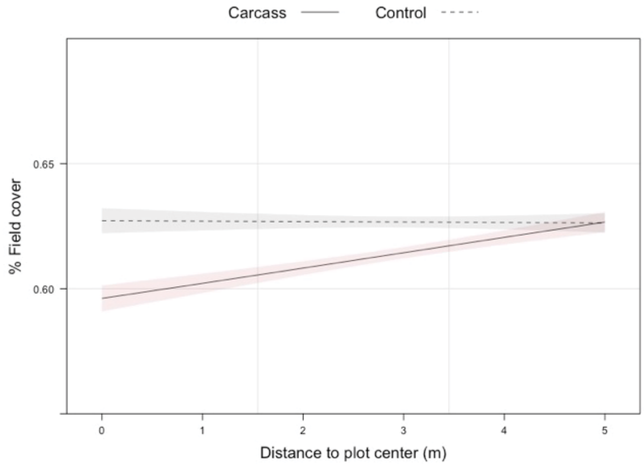

Figure 6 *Predicted field cover of vascular plants at different distances from the centre of the moose carcasses in the boreal forest in South-Central Sweden.*

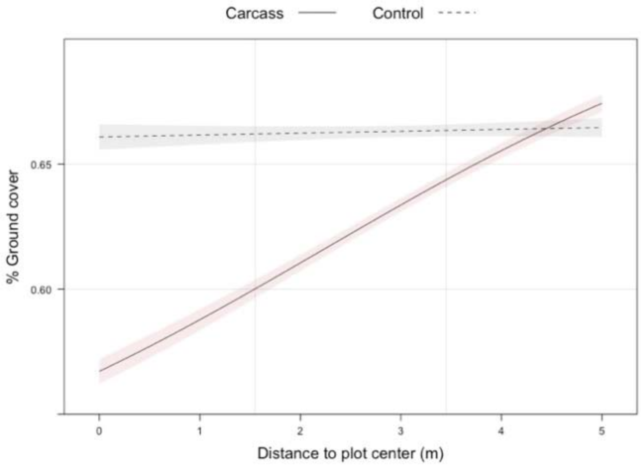

Figure 7 *Predicted ground cover of bryophytes and lichens at different distances from the centre of the moose carcasses in the boreal forest in South-Central Sweden.*

Table 3 *Estimates of the most parsimonious models for field cover of vascular plants and ground cover of bryophytes and lichens. The model to assess field cover is represented in the upper half of the table, the lower half shows the results for the ground cover model.*

Model terms	Estimate	Standard error (SE)	z-value	p-value
Field cover				
Type:control	0.889	0.069	-4.268	<0.001
Distance	0.157	0.015	10.266	<0.001
Microtopography	0.025	0.008	3.358	<0.001
Type:Distance	-0.215	0.021	-10.056	<0.001
Ground cover				
Type:control	1.87	0.078	24.133	<0.001
Distance	0.422	0.016	25.399	<0.001
Microtopography	-0.035	0.008	-4.474	<0.001
Year2015	-1.415	0.486	-2.022	0.003
Type:Distance	-0.415	0.024	-17.277	<0.001

Species composition

For the GNMDS analysis, two identical solutions were obtained after 200 iterations on both the three and four dimensions' solution. I chose to use three dimensions based on Kendall´s rank correlation coefficients τ, as the three and four dimensions were correlated $\tau = 0.92$ ($p < 0.001$). The first NMDS and DCA axis were strongly correlated ($\tau = 0.79$, $p < 0.001$) and indicated that both methods identified the same main gradient structure in the data. Comparisons of the other axes showed moderate to high correlation (axis 2: $\tau = 0.33$, axis 3: $\tau= 0.53$, both $p < 0.001$). For further analysis, I chose to use DCA since it provided biologically more intuitive results on the second axis.

DCA axis 1 (gradient length 4.0087 SD units) represented a gradient in forest age (Figure 9). The gradient ran from mature forest (Figure 8, left) to clear-cut forest (Figure 8, right), with secondary thinning and young forest in the centre of the axis (Fig 8, middle). This axis separates species accordingly (Fig 8). For example, *Goodyera repens* is a species that is only found in older forests, whereas, *Polytrichum commune* is a species often found on clear-cuts. DCA axis 2 (gradient length 3.0846 SD units) separated the most disturbed carcass centre plots from plots further from the other carcass plots and control plots (Figure 9). The second axis separated pioneer species (e.g., *Pohlia nutans, Ceratodon purpereus, Betula pendula/pubescens, Polytrichum juniperinum, Solidago viraugea, Rubus idaeus, Rubus saxatilis*) (top), from species common on the undisturbed forest floor (middle) (*Vaccinium spp., Hylocomnium splendens, Dircranum spp., Cladonia spp.),* and species that were found in the oldest and densest forest (bottom) (*Goodyera reprens*). DCA axis 3 showed a gradient from lichen-rich pine forest via mixed herbs/Vaccinium-spruce forest to spruce forest located near a bog, indicating that this a gradient in moisture availability.

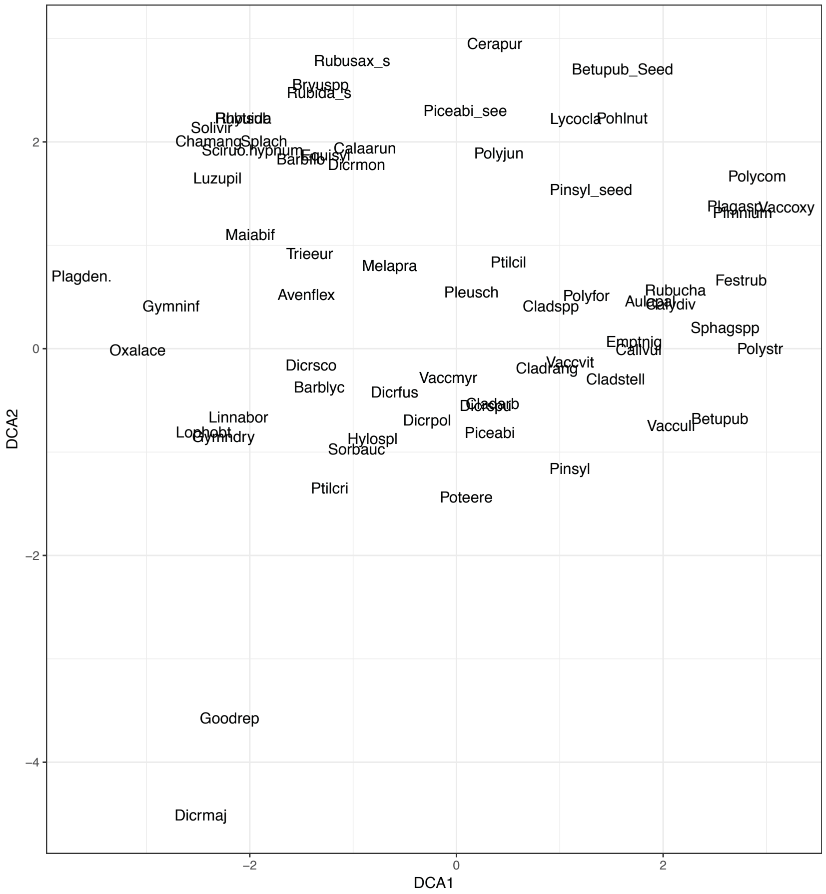

Figure 6 *The first gradient (DCA1) ran from mature forest on the right, young forest in the middle and a clear-cut on the left. The second gradient (DCA2) showed species common on the disturbed carcass plots (top) and species common on the undisturbed forest in the middle, whereas two species that were only abundant in the oldest forest were located at the bottom of the second DCA axis.*

The environmental vectors added to the DCA plot revealed that higher levels of nitrogen, carbon and phosphorus were positively correlated with the most disturbed carcass centre plots (Fig 9). No relationship for other soil nutrients were found. In addition, less canopy cover showed a slight positive correlation with the disturbed plots. In contrast, both field cover of vascular plants and ground cover of bryophytes and lichens, and distance to centre was negatively correlated with the disturbed carcass plots.

The PCCA analysis revealed that there was a difference in species composition on carcass and control sites, when conditioned for location ($p < 0.001$). The average LC plot score for carcass and control (centroids) were clearly separated along the CCA-axis (carcass -1.035, control 0.966).

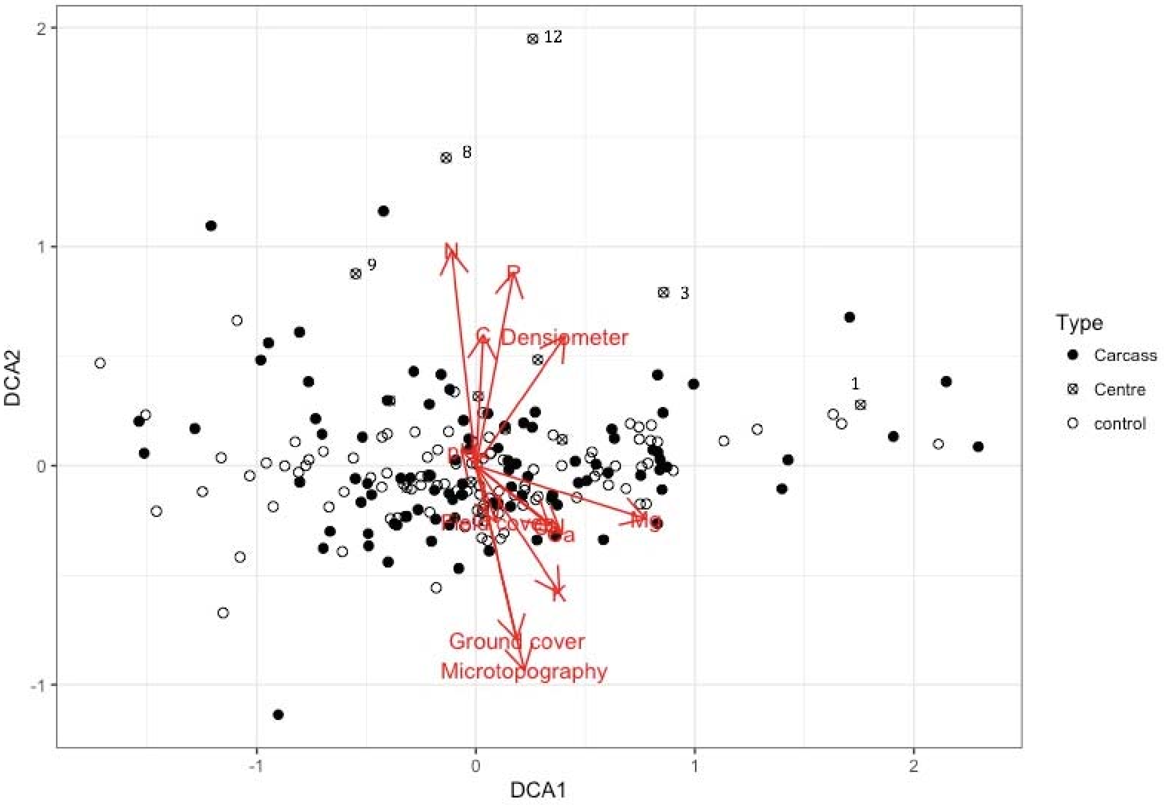

Figure 7 *DCA with environmental vectors revealed a correlation for disturbed carcass plots with higher levels of nitrogen, phosphorus and carbon. Canopy cover also showed a slight correlation. Some centre-plots are marked with site number, for information see Table 1. Length of the environmental vectors can be found in Appendix 2.*

Indicator species

Of the 62 species recorded, six were classified as indicators species. Five species were indicators of carcass-centre plots and one species was an indicator of carcass (outside plot centres) or control plots (Table 5). The species with the highest indicator value for carcass centres was the moss *Pohlia nutans* (Indicator value 66.6, p = 0.001). In addition, tree seedlings of *Betula* spp. and *Pinus sylvestris* had high indicator value for carcass centres (Table 5). Mosses *Bryum* and *Plagiomnium ellipticum* occurred more often on the carcass centre plot, but the sample size was also very low. The lichen *Cladonia arbuscular* occurred significantly more often on carcass and control plots compared to carcass centres. However, most species did not belong to any of the groups, and 17 of the species occurred in all three groups of sites. Moreover, the indicator analysis for growth form, showed that tree seedlings were the only growth form with significant differences in occurrence at carcass centres compared to other carcass plots and control plots (p <0.001).

Table 5 *The six different indicator species, with the most indicative species (Pohlia nutans) on the top. Five of the species were indicators of carcass-centre plots, while only one species seemed to avoid these plots. The rest of the table is in Appendix 3.*

	Freq	IV	P	Carcentre	Carcass	Control	GF
Pohlia nutans	31	66.6	**0.001*****	**76/58**	20/19	4/5	b
Betula spp. seedling	6	47.2	**0.002****	**90/25**	8/2	2/1	ws
Pinus sylvetris seedling	22	49.4	**0.007****	**74/33**	18/11	8/6	ws
Bryum sp.	3	40	**0.007****	**97/17**	3/1	0/0	b
Cladonia arbuscula	58	53.3	**0.042 ***	0/0	**36/19**	**64/37**	l
Plagiomnium ellipticum	2	28	**0.048***	**94/8**	6/1	0/0	b

Variation partitioning

The final PCCA model to quantify the amount of explained variation in species composition per included carcass (carcass/control), soil related variables (phosphorus, calcium, pH, magnesium, potassium, substrate depth, mineral layer depth, total soil depth), and habitat (canopy cover elevation, slope, aspect, forest type) as explanatory variables. The model explained 27.5 % of the variation in species composition with the environmental variables used (Total Inertia 4.98, unexplained 3.62). Of the explained variation, habitat explained the largest fraction of the variation in species composition (42 %; Fig 8). The second largest group was the soil related variables (20%; Fig 8). Third, was the shared variation between soil related variables and habitat (19 %; Fig 8). Carcass explained 11 % of the variation and had no shared variation with the other groups according to the analysis. Lastly, site explained 9 %.

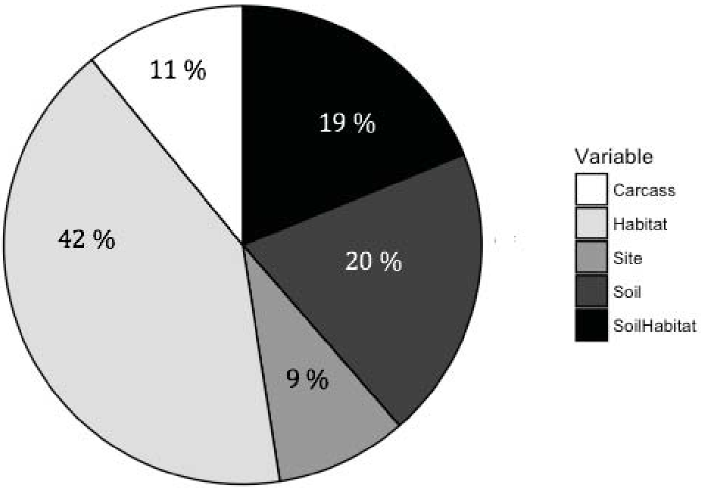

Figure 8 *The proportion of explained variation in the species composition by the different groups of explanatory variables. The carcass group contained carcass/control. In the habitat group, canopy cover elevation, slope, aspect, forest type was included. While phosphorus, calcium, pH, magnesium, potassium, substrate depth, mineral layer depth, total soil depth belonged to the soil-related variables*

DISCUSSION

My research produced three key findings. First, large carnivore kills create local and intense disturbance to vegetation, and decrease both field and ground cover (H1), at least in the first two years after the kill occurred and with decreasing distance to the carcass centre. Second, carcasses affected vegetation composition in its entirety, although the effect seemed to be most pronounced locally (at carcass plot centre) and rather modest. DCA revealed that forest age was the most important gradient regarding species composition, and disturbance at the carcass site was the second most important factor (H2). Third, tree seedlings abundance was greater at carcasses and three species of moss (*P. nutans*, *Bryum* sp., *P. ellipticum*) occurred more often on the carcass centre plots, whereas only one lichen species was significantly negatively affected by carcass presence (H3).

Ground- and field cover were significantly lower at carcass site compared to the control sites, and the effect was most profound at the carcass plot centres (Figure 3af). Carcass remains, mostly hair, covered the understory vegetation, thereby killing it (Barton et al. 2013a; Carter et al. 2007). Hair decomposes slowly (Barton et al. 2013a; Carter et al. 2007) and even one year after death, there was still noticeable amounts of hair present on several sites (Fig 3). These results concur with Towne (2000) and Bump et al. (2009b), who also report decreased plant cover during the first years of carcass decomposition. As cover is reduced, so is competition for nutrients and light. Reduced plant cover due to disturbance creates ‘windows of opportunity’ for certain species/growth forms, and appears to affect species composition in its entirety. Bump et al (2009b), for example, also found that the reduced cover of the herbaceous layer changed competitive interactions, allowing tree seedlings to establish (Bump et al. 2009b). Towne (2000) showed that cover was significantly reduced one year after an animal´s death, but increased to over pre-disturbance levels two years after death and remained higher for the next years. I found that carcasses from 2015 had significantly lower ground cover of mosses and lichens than those from 2014. This demonstrated that revegetation already had a significant effect two years after disturbance. As the carcasses did not remove any of the humus layer and mainly just killed the plants growing on the ground, revegetation may occur rapidly. Plants with clonal growth recvore more rapidly in less strongly disturbed patches (Rydgren et al. 2004) and in smaller patches (Jonsson & Esseen 1998). Both *H. splendens* (Callaghan et al. 1978) and *P. schreberi (Huttunen 2003)* are dependent on clonal growth and seldom reproduce sexually. Site disturbed by the carcasses were rather small (<2m^2) and revegetation from the surrounding vegetation appeared to be fast. When the wolves kill a moose, a fight occurs, which disturbed the ground to a greater degree than the disturbance area produced by the presence of the carcass alone (Andrés Ordiz, pers comm). The observed disturbed areas were relatively small, suggesting fast revegetation.

Both the DCA and NMDS analysis revealed that forest age was the most important gradient regarding variation in species composition. Forest age reflects the amount of available light, moisture and nutrients, which are all important factors in explaining vegetative variation in the boreal forest (Økland 2000). The variation partitioning model explained only 27.42 % of the total variation, but due to unmeasured environmental variables, complex spatial relationships, stochasticity in biological processes, and noise, it is recommended to avoid too much speculation about the unexplained variation (Rune Halvorsen & Wilson 2003). Therefore, I rather focused on the relative amount of variation explained by the different components. The variation partitioning analysis showed that the habitat variables explained 46 % of the variation. For comparison, carcasses explained 11 %. This concurred with the DCA analysis, which also emphasized that habitat / forest type was more important in determining species composition. This is mainly because forest age, affects a much larger scale than carcasses. Moreover, soil and the soil/habitat explained a good portion of the variation, 20% and 19 %, respectively. Soil nutrients and soil depth are important factors contributing to the aboveground biota (Wardle et al. 2004). Soil and habitat are often very closely linked (e.g. thinner soil layer and less nutrient are common in the drier lichen forests compared to the bilberry forests). Site also influenced species composition. This is variation that could not be explained by any of the other variables and can be attributed to the individual environmental conditions at each site. As I sampled a great variety of habitats and environmental conditions, the species found reflected the individual sites to a high degree. For example, I only sampled in one clear-cut and one mature forest, so the species found here reflected the conditions on that particular sites (e.g. pine forest/spruce forest/mixed forest). The impact from the carcasses on the vegetation appears to be rather modest, even though it appeared that some species may have been positively affected, as shown by the second DCA axis.

The second DCA axis separated newly disturbed plots and undisturbed plots (Figure 8). This axis also reflected the amount of ground cover on the different plots (Figure 9). It separated species regenerating from the diaspore bank (*Pohlia nutans, Ceratodon purpereus, Betula pendula/pubescens, Polytrichum juniperinum, Pinus sylvestris*) and species found on the undisturbed forest floor (*Goodyera repens, Dicranum majus*) (Figure 8). This indicated that carcasses are important for the species composition of the forest floor, albeit less strongly than forest age. Many species present in the soil diaspore bank are not able to compete with the few competitive species present in the above-ground vegetation (*H. splendens, P. schreberi, Vaccnium* spp.*)* (Jonsson 1993). However, when these competitive species are removed, there appears to be an opportunity for the species present in the soil diaspore bank to establish.

Both the DCA analysis and the indicator analysis showed that *Betula* and *Pinus* seedlings were more abundant on carcass-centre plots (Figure 8, Table 5). This is in line with findings by Bump et al. (2009b), who also found an increased abundance of tree seedlings on carcass plots. When the cover of the dominant species is reduced, the competition for light, nutrients and space is reduced simultaneously, which are all important for seedling growth and survival (Beckage & Clark 2003; Gray & Spies 1997). Beckage and Clark (2003) found that seedling survival in the southern Appalachian forest increased in canopy gaps, with removal of understory vegetation and with fertilization. Survival increased the most when all treatments were present. The DCA-plot with the environmental vectors (Figure 9) indicated a correlation between disturbed carcass centre plots and higher levels of nutrients, light and less ground cover. As tree seedlings were more abundant in the carcass centre plots, this may suggest that there is an additive effect of nutrients, light and less competition. In contrast, a study from the boreal forest in Finland concluded that ground disturbance was the most important factor for seedling establishment (Kuuluvainen & Juntunen 1998). In the boreal forest, competition for light has been seen as less important, as more light usually reaches the ground floor due to the high amount of conifers (Kuuluvainen & Juntunen 1998). On the other hand, the ground is usually covered with a continuous carpet of feather mosses (*H. splendens, P. schreberi*), which are almost impenetrable for other species, thus making competition for space an important factor (Jonsson 1993; Kuuluvainen 1994). Small-scale disturbances disrupt the continuous bryophyte carpet, creating space free from potential competitors and thus, making it more likely for less competitive species to establish. The successional patterns after a disturbance are highly determined by the soil propagule bank (Jonsson 1993). In addition to seedlings of Betula and Pinus, I found three species of moss (*P. nutans, Bryum* sp., *P. ellipticum*) to be more abundant on the carcass centre sites. *P. nutans* and *Bryum* sp. have earlier been found to be present in the soil diaspore bank (Jonsson 1993; Rydgren & Hestmark 1997). In addition, *Polytrichum* spp. and *Betula* spp. have also been found to be present in the diaspore bank (Jonsson 1993). Moreover, these species have been recognized as pioneer species, emphasizing the importance of the diaspore bank, in relation to successional patterns (Jonsson 1993; Rydgren & Hestmark 1997; Rydgren et al. 2004).

The result of this study have several common features with studies of vegetation following tree uprooting's. Jonsson and Esseen (1990) found that uprooting by trees releases competition and makes it possible for less competitive species to establish. They found *Pohlia* spp. and *Polytrichum* spp. to be important species on the disturbed forest floor. The indicator analysis I conducted, indicated *P. nutans* as the species most linked to carcass centre plots (Table 5). In addition, the DCA-plot identified *P. juniperinum* as one species linked to carcass centre plots (Figure 8). In a posterior experimental study, seedlings of *Pinus* and *Betula* were found to be more abundant on disturbed sites (Jonsson & Esseen 1998). In contrast to disturbance from carcasses, uprooting of trees also uncovers mineral soil and creates a larger variety of microhabitats. Earlier studies have reported a higher diaspore bank in the mineral layer compared to the humus layer, which may explain the extreme diversity seen on uprooted trees and not at the carcass sites (Jonsson & Esseen 1990). Additionally, uprooting creates a gap in the canopy, increasing the solar radiation reaching the ground, which may affect seedling and bryophyte establishment (Kuuluvainen 1994). As neither of this occurs at the carcass sites, I expected the response to be less dramatic.

The indicator analysis (Table 5) revealed that the only growth form related to carcasses was seedlings. This is in line with some previous findings (Bump et al. 2009b), but contrasts with other. Barton et al. (2013b) found a greater dominance of graminoids on carcass sites in an Australian *Eucalyptus* forest. Danell et al. (2002) found a great effect on the vegetation surrounding the carcass, increasing productivity. Towne (2000)also reported an increase in the abundance of the perennial grass *Agropyron smithii* at carcass sites. Additionally, Towne (2000) found that biomass increased as much as six times at one carcass site. Both studies reported increased levels of soil nutrients at the carcass sites, which indicate the effect the soil nutrients may have on the vegetation (Towne 2000, Danell et al. 2002). The DCA analysis with environmental variables (Figure 9) showed that there was a correlation with higher nitrogen, phosphorus and carbon, as well as lower C:N ratio and carcass sites. This is in agreement with a parallel soil study (Stengeli, in prep) that found lower C:N ratios at the carcass site compared to the control sites and trends in C and N soil content. However, none of the other soil nutrient analysis showed significant results. There may be several explanations for this. First, for all nutrients except nitrogen and carbon, the samples where pooled, mixing the carcass-centre soil samples with those five meters away. As for nitrogen, the turnover time may have been too quick, as we conducted our soil analysis more than one year, at least, after death of all the moose. Melis et al. (2007) reported that elevated nitrogen levels only occurred the first year. Barton et al. (2013b) reported soil nitrogen to be 200 % higher than the control site 12 weeks after death and 70 % higher after 26 weeks, which also indicates a fast turnover time. Towne (2000) reported elevated nitrogen levels up to two years after the death of the animal, but in this experiment, no predation or scavenging was present. These results agree with Stengeli (in prep.), which found that the CN ratio was lower in 2015 than 2014 at carcass sites. Melis et al. (2007) reported higher levels of calcium in the first three years after death. It is likely that calcium comes mainly from bones and is recycled more slowly than other nutrients (Melis et al. 2007). As we only sampled one and two-year-old carcasses, higher levels of calcium may not have been present in the soil yet. Another explanation is that scavengers move bones away from the original carcass sites, transporting nutrients to distant areas (Melis et al. 2007).

In this study, I could not detect any gradient along the distance in species composition. In the parallel soil study, no such gradient was detected either. My results concur with those of Melis et al. (2007), who reported that the soil nutrients varied irregularly, which suggests an effect at the centre of the carcass, but no clear pattern along its gradient. Both Towne (2000) and Danell et al. (2002) reported a clearer gradient, even though the response was asymmetric. There may be different reasons why there was no clear pattern in the soil or vegetation at the carcass sites and surroundings. First, the rate of decomposition is determined by accumulated degree days (Carter et al. 2007). For a 68-kg human cadaver it took 16 days to reach the final stages of decay at a temperature of 25°, whereas it took up to 80 days at 5˚C (Carter et al. 2007). The moose in our study were killed between 1. April and 22. June and around this time the average temperature in the study area is 2.1°C in April and 13.4°C in June (*SMHI Klimatdata Sverige* 2016). Because of the low temperature, it is likely that cadaver decomposition went slow and more carcass material was available for scavengers (Carter et al. 2007; Melis et al. 2007). Importantly, most of each carcass (50-90 % in average) was consumed in 3-4 days (Ordiz, Pers comm) and temperature may be of less importance than if an animal died of reasons other than predation and scavengers took some time to find it. Although not tested, the clearest effect on the vegetation seemed to be from carcasses that were not fully consumed and where most of the dead animal was left to cover the underlying vegetation. The composition of the vegetation on the centre plot of site 12 and 8 differed the most from the surrounding vegetation, suggesting that these carcasses had the greatest effect on the vegetation (Figure 8). At these two sites, the carcasses were 60 and 70 % consumed, respectively (Table 1). For site number 12, no bears were detected on any cameras and the only scavenger detected was the red fox. For site 8, a bear was detected on the camera, but that was about one month after the death of the animal. In contrast, there were two additional carcasses that were scarcely consumed (Site 4 and 5; Table 1), but on both these sites brown bears were detected. On site number 4, the bear appeared on the camera a few weeks after the camera was put up by SKANDULV. On this site, the bear likely dragged the carcass away from the original spot, which is probably influenced the disturbance from the carcass at the original site. At site number 5, a brown bear was detected the same day as the camera was put up. Here too, the bear may have moved the carcass as well. On the rest of the sites, between 80 and 99 % of the carcass was consume. This suggests that the consumption by wolves and scavengers is important for the outcome of disturbance. Even though the evidence is scarce, it seems plausible to suggest that the additional scavenging by brown bears, reduced the disturbance effect from the carcass.

I have been looking on adult moose and wolf predation bias towards calves and juveniles (Sand et al. 2008; Sand et al. 2012), hence the local effect on soil nutrients and vegetation of individual carcasses caused by wolf predation might be lower than reported here. Towne (2000), for example, found a clearer gradient in nutrients dispersed on adult bison carcasses compared to juveniles, and it is generally acknowledged that larger biomasses generate more pronounced effects on soil and vegetation. I chose to use only carcasses of $\geq$1 year-old moose because it seem plausible that there would be more nutrients to spread from these carcasses. Neonate calves are often consumed by predators within hours and the effect on the vegetation and soil nutrients may be negligible (Ordiz, pers comm).

Apex carnivores affect ecosystem processes through altering population dynamics and behaviour of their prey (Estes 1995; Ripple & Beschta 2012b; Terborgh et al. 2001). This study highlights the more direct way apex predators influence lower trophic levels and adds to the body of evidence for apex carnivores' role in the ecosystem (Holtgrieve et al. 2009). Predation by wolves distribute ungulate carcasses that create intense local disturbances and modulate heterogeneity in soil nutrients, that affect plant composition (Bump et al. 2009a). As most apex carnivores are under strict management regimes, studies, like this one, may help create awareness around conservation of large carnivores.

CONCLUSION

My research points to that wolves through their predatory behaviour affected the composition of the vegetation, although very local and rather modest. The carcasses seem to disrupt the dominant ground cover of mosses and lichens and change competitive interactions among the vascular plants, bryophytes and lichens. Concurrent with other studies, the carcasses seem to facilitate tree seedlings and a few pioneer moss species through disturbance. My results suggest that the amount of carcass material left by the wolves is an important component for the further disturbance. Scavenger activity, especially bears, also seem to affect the disturbance intensity, as they often move the carcass away from the original site. This study emphasizes that top-level carnivores may affect the composition of the vegetation, and as other small-scale disturbances are rare, this may increase the importance of apex carnivores as disturbances.

As this study had some limitations, I suggest doing a follow up study. First, I visited the carcasses >1 year after the animals' death, which limited our capacity to see effects on the vegetation at early stages. Because it proved too difficult to find the exact spot of the 2011 carcasses, we did not sample vegetation at these sites. If possible, it would be nice to mark the carcasses just after the moose were killed and then do vegetation analysis a few months after, as well as study the effects the next years. I would also find it interesting to further investigate the effects from carcasses killed by predators and carcasses that died for other reasons, to examine the effect of the predator behaviour and to find out if it is the disturbance from the carcass or from the kill that is the most important factor. Additionally, it would be of interest to study the effects on soil and vegetation of the carcasses of calves/juveniles, since juveniles are important in terms of predation rates.

Apex carnivores affect ecosystem processes through altering population dynamics and behaviour of their prey. This study highlights the direct effect of wolf predation on the soil and vegetation composition and adds to a growing pile of evidence of apex carnivores' role in the ecosystem. As most apex carnivores are under strict management regimes, studies, like this one, may help create awareness around the conservation of large carnivores.

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Appendix 1

Ground cover model	Df	AICc	ΔAICc	Weight
Type + Distance	5	4781.2	2.06	0.124
Distance + Type + Microtopography + Densiometer + Year + Distance:Type	9	4781.2	2.09	0.122
Distance + Type + Distance:Type	6	4781.8	2.70	0.090
Distance + Type + Densiometer + Distance:Type	7	4782.2	3.10	0.074
Distance + Type + Year + Distance:Type	7	4783.3	4.16	0.043

Field cover model	Df	AICc	ΔAICc	Weight
Distance + Microtopography + Type + Distance:Type	7	7936.2	4.18	0.079
Distance + Type + Densiometer + Microtopography + Distance:Type	8	7938.0	5.92	0.033
Distance + Type + Year + Distance:Type	7	7959.2	27.18	0.000
Distance + Type + Year + Densiometer + Distance:Type	8	7960.8	28.75	0.000
Distance + Type + Distance:Type	6	7963.5	31.43	0.000

Appendix 2

***Appendix 2** Overview of the different environmental explanatory variables, their position in the DCA plot, as well as the length of the arrows.*

	DCA1	DCA2	Length
Distance	-0,0239	-0,9675	0,96781
P	0,1797	0,8872	0,90521
Ca	0,4128	-0,3787	0,56018
Mg	0,9208	-0,3895	0,99976
pH	-0,1596	0,3023	0,34187
Densiometer	0,5855	0,7294	0,93531
Microtopography	0,2370	-0,9619	0,99067
K	0,4918	-0,8139	0,95090
C	0,0308	0,6683	0,66902
N	-0,1072	0,9938	0,99957
CN	0,4427	-0,4964	0,66509
Slope	-0,9638	0,1231	0,97160
Elevation	-0,3836	0,9216	0,99823
Substrate	0,5318	-0,1410	0,55018
Mineral	-0,7289	-0,1168	0,73819
Soil depth	-0,8418	-0,5014	0,97981
Ground cover	0,1880	-0,7852	0,80743
Field cover	0,0952	-0,2217	0,24129

Appendix 3

	Freq	IV	P	Centre	Carcass	Control	GF	Abbrevations
Ceratodon purpereus	2	28.3	0.056 .	**96/8**	4/1	0/0	B	Cerapur
Lycopodium clavatum	4	25.8	0.097 .	80/8	20/3	0/0	f	Lycocla
Calamagrostis arundinaticea	10	28.5	0.1	63/8	34/8	3/1	g	Calaarun
Rubus saxatilis shoot	3	26.1	0.1	82/8	18/2	0/0	f	Rubusax_s
Picea abies seedling	2	27.2	0.103	89/8	11/11	0/0	ws	Piceabi_seed
Sciruo-hypnum spp.	23	36.3	0.118	34/17	45/17	21/5	b	Sciuro-hypnum
Vaccinium oxycoccus	3	20.4	0.138	50/8	44/1	6/1	ds	Vaccoxy
Oxalis acetosella	13	26.5	0.197	10/8	16/3	74/8	f	Oxalace
Rubus idaeus (new shoot)	4	17.6	0.223	0/0	100/4	0/0	ws	Rubuida_s
Aulacomium palustre	9	23.1	0.225	0/0	86/6	14/3	b	Aulapal
Dicranum montanum	33	39.3	0.253	41/33	39/18	20/11	b	Dicrmon
Sphagnum spp.	18	29.8	0.253	0/0	71/12	29/6	b	Sphagspp
Chamerion angustifolium	3	17.6	0.264	0/0	100/3	0/0	f	Chamang
Splachnum spp.	2	14.4	0.308	0/0	100/2	0/0	b	Splach
Lophozia obtusa	2	14.4	0.315	0/0	100/2	0/0	b	Lophobt
Equisetum sylvaticum	2	14.4	0.316	0/0	100/2	0/0	f	Equisyl
Dicranum spurium	4	19.2	0.317	0/0	0/0	100/4	b	Dicrspu
Maiantemum bifolium	25	35	0.38	0/0	47/13	53/12	f	Maiabif
Luzula pilosa	24	34.2	0.397	0/0	51/8	49/15	g	Luzupil
Rhytidiadelphus subpinnatus	1	10.2	0.489	0/0	100/1	0/0	b	Rhytsub
Betula pendula/pubescens	3	12.6	0.571	0/0	77/2	23/1	w	Betula_seedling
Rubus chamaemorus	2	13.6	0.585	0/0	0/0	100/2	f	Rubucha
Polytrichastrum formosum	14	26.1	0.670	0/0	72/10	28/5	b	Polyfor
Polytricum strictum	12	24	0.724	38/8	40/7	22/4	b	Polystr
Calypogeia spp.	9	21	0.870	0/0	63/6	37/3	b	Calyspp.
Ptilidium ciliare	5	15.7	0.98	0/0	20/2	80/3	b	Ptilcil
Vaccinium uligionosum	6	17.1	1.000	0/0	67/4	33/2	ds	Vacculi
Solidago viraugea	6	17.1	1.000	0/0	48/3	52/3	f	Solivir
Picea abies	3	12.1	1.000	0/0	27/1	73/2	w	Piceabi
Sorbus acuparia	5	15.6	1.000	0/0	53/3	47/2	w	Sorbacu
Pinus sylvestris	2	9.9	1.000	0/0	53/1	47/1	w	Pinsyl
Potentilla erecta	1	9.6	1.000	0/0	0/0	100/1	f	Poteere
Goodyera repens	2	9.9	1.000	0/0	53/1	47/1	f	Goodrep
Dicranum majus	3	12.1	1.000	0/0	49/1	51/2	b	Dicrmaj
Polytrichum commune	2	9.9	1.000	0/0	69/1	31/1	b	Polycom
Plagiothecium laetum	2	9.9	1.000	0/0	46/1	54/1	b	Plagden
Barbilophozia floerki	3	12.1	1.000	0/0	69/2	31/1	b	Barbflo
Barbilophozia lycopoides	18	29.7	1.000	0/0	32/7	68/10	b	Barblyco
Gymnocolea inflata	4	14	1.000	0/0	22/2	78/2	b	Gymninf
Gymnocarpium dryopteris	1	9.6	1.000	0/0	0/0	100/100	f	Gymndry
Plagiochila asplenoides	2	9.9	1.000	0/0	53/1	47/1	b	Plagasp
Cladonia stellaris	2	9.9	1.000	0/0	53/1	47/1	l	Cladste
Empetrum nigrum	21	31.1	N/A	5/8	47/9	48/10	ds	Empenig
Vaccinium myrtillus	176	90	N/A	25/67	37/80	38/84	ds	Vaccmyr
Vaccinium vitis-idea	169	88.4	N/A	22/66	38/83	40/75	ds	Vaccvit
Calluna vulgaris	56	50.9	N/A	15/8	45/31	40/23	ds	Callvul
Melampyrum pratense	41	43.5	N/A	10/8	50/22	40/18	f	Melapra
Trientalis europea	26	34.6	N/A	10/8	55/14	35/11	f	Trieeur
Linnea borealis	42	44	N/A	8/17	43/20	49/19	f	Linnbor
Avenella flexuosa	104	69.4	N/A	21/25	35/43	44/55	g	Avenbor
Festuca rubra	13	24.5	N/A	33/8	38/7	29/5	g	Festrub
Dicranum fuscesens	83	62	N/A	17/25	43/46	40/33	b	Dicrfus
Dicranum scoparium	88	63.8	N/A	30/42	33/42	37/40	b	Dicrsco
Dicranum polysetum	146	82.2	N/A	10/33	39/65	51/74	b	Dicrpol
Hylocomium splendens	146	82.2	N/A	16/42	44/72	40/66	b	Hylospl
Ptilitum crista-crastensis	44	45.1	N/A	39/25	32/19	29/21	b	Ptilcri
Pleurozium schreberi	203	97	N/A	28/83	34/93	38/96	b	Pleusch
Polytrichum juniperinum	25	34	N/A	32/17	46/12	22/10	b	Polyjun
Cladonia rangiferina	59	52.2	N/A	9/17	42/26	49/29	l	Cladrang

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