The direct and indirect relation between ungulates on small mammals

Michael Wentzel

Master's thesis • 60 hp
Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish, and Environmental Studies
Examensarbete/Master's thesis, 2020:15
Umeå 2020

The direct and indirect relation between ungulates on small mammals

Michael Wentzel

Supervisor:	**Joris Cromsigt, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies**
Assistant supervisor:	Tim Hofmeester, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Assistant supervisor:	Nannet Fabri, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Examiner:	Frauke Ecke, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies

Credits:	60 hp
Level:	Second cycle, A2E
Course title:	Master's thesis in Biology, A2E – Wildlife, Fish, and Environmental Studies
Course code:	EX0970
Course coordinating dept:	Department of Wildlife, Fish, and Environmental Studies
Place of publication:	Umeå
Year of publication:	2020
Cover picture:	Rolf Segerstedt
Title of series:	Examensarbete/Master's thesis
Part number:	2020:15

Keywords:	Small mammals, ungulates, vegetation cover, food competition, path analysis, direct, indirect, canopy cover, Sweden

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Wildlife, Fish, and Environmental Studies

Archiving and publishing

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. When you have approved, metadata and full text of your thesis will be visible and searchable online. When the document is uploaded it is archived as a digital file.

☑ YES, I hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work. https://www.slu.se/en/subweb/library/publish-and-analyse/register-and-publish/agreement-for-publishing/

☐ NO, I do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.

Abstract

Ungulates are increasing in Europe, including Sweden and can cause changes to forest structure and forest-dwelling animals. This study is focused on the relation between various ungulate species and small mammal abundance in Swedish forests, through the alteration of ground vegetation cover and directly through food competition. The relation between canopy cover and ground vegetation cover, and thus small mammals is also explored.

Path analysis revealed ground vegetation cover was positively related with small mammal abundance, yet no relation was found between ungulates and ground vegetation cover and therefore no indirect relation between ungulates and small mammals. Interestingly, the significant relation between vegetation cover and small mammals was lost when the species were modelled individually, possibly due to small sample size. Certain ungulates were directly correlated with small mammals when modelled at the species level. Yellow-necked mice was positively correlated with wild boars and fallow deer densities and bank voles were negatively correlated with roe deer density. Ground vegetation cover was negatively correlated with canopy cover; thus canopy cover was indirectly negatively correlated to small mammal abundance.

This study shows that vegetation cover is positively correlated with small mammals but does not suggest an indirect relation between ungulates and small mammals. The study also highlights the complexity of the studied forest ecosystem, where certain individual ungulate species directly correlate with individual small mammal species. Animal diversity, human health and ecosystems are influenced by small mammals, and vegetation cover should therefore be considered when applying management actions that increase forest biodiversity and decrease tick-borne diseases.

Keywords: small mammals, ungulates, vegetation cover, food competition, path analysis, direct, indirect, canopy cover, Sweden

Table of contents

List of tables

List of figures

Abbreviations

FPG	Faecal Pellet Group
SLU	Swedish University of Agricultural Sciences

1. Introduction

Europe has witnessed an increase in densities and range of wild ungulate species (Apollonio, Andersen, & Putman, 2010). This is also the case in Sweden, where the population of moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) have grown over the past decades. Several reasons for this increase include milder winters, management actions, and changes in forestry practices (Kuijper et al., 2009).

Increasing ungulate populations can change forest structure and composition, which occur through grazing, browsing, trampling, fraying, stripping, uprooting, defecating and seed dispersal (Gill & Beardall, 2001; Ramirez et al., 2018; Rooney, 2001). Generally, high ungulate densities have been shown to shift the plant community dominated by palatable species to a community with unpalatable species, because ungulates select palatable plants which give unpalatable plants a competitive advantage and can therefore increase in abundance (Kirby, 2001). A study from the UK, which looked at the vegetation changes of a forest for 22 years after being relieved of high browsing pressure, found the area change from a sparse flora community composed of unpalatable species like bracken (*Pteridium aquilinum*) to a community dominated by palatable species such as bramble (*Rubus fruticosus*) (Putman et al., 1989). However, browsing does not necessarily shift the plant community towards unpalatable plants. Palatable species can sometimes increase in abundance in nutrient-rich systems due to the selection of ungulates on *patches* of vegetation, i.e. not on individual plants, and consequently outcompete browsing-intolerant, unpalatable plant species (Cromsigt & Kuijper, 2011). Another response to high ungulate densities is that grasses and grass-like species can increase in abundance due to their tolerance to grazing and therefore have a competitive advantage over other plants (Kirby, 2001). Lastly, browsing on tree seedlings can delay succession from an open field to a closed canopy and tree regeneration can even be completely prevented at high ungulate densities (Flowerdew & Ellwood, 2001).

These changes to the forest consequently have an impact on other forest animals. For instance, overall bird abundance decreased and species composition changed with increasing deer density in a North American study (Gill & Fuller, 2007). In this study, bird species that highly depend on understory vegetation for food and shelter decreased and species that prefer a more open understory increased in abundance. Another study found invertebrates impacted by ungulate browsing, where the populations were affected according to their preferred habitat and the change ungulates made to this habitat (Stewart, 2001). For example, the ground beetle *Abax parallelepipedus* prefers a habitat with a closed canopy and more ground cover and was therefore more abundant where ungulates were absent, contrasting to the beetle *Nebria brevicollis*, which prefers a habitat with low amount of cover and was only found in grazed areas (Putman et al., 1989). And finally, several studies have shown that small mammal communities are affected by ungulates (Buesching et al., 2011; Keesing, 1998; Moser & Witmer, 2000; Muñoz et al., 2009; Parsons et al., 2013; Putman et al., 1989; Smit et al., 2001).

Ungulates can directly and indirectly influence small mammal abundance (Flowerdew & Ellwood, 2001). The indirect effect occurs through the alteration or removal of habitat, which can impact cover, food availability and access to stable burrows. The direct effect occurs through direct competition over food and feeding of wild boars on small mammals (Amori et al., 2016; Flowerdew & Ellwood, 2001). Consequently, inter-specific competition between small mammal species can aggravate the effects of ungulates on small mammals. The direct and indirect pathways are shortly reviewed.

Ungulates can change the habitat in several ways that in turn can impact small mammals. As previously described, ungulates can change the flora community, consequently affecting food availability for small mammals (Flowerdew & Ellwood, 2001). In the study example from the UK used before, they discovered that bramble became more abundant after removing ungulates from the area (Putman et al., 1989). Bramble is a source of food for some small mammals, thus an increase in ungulate density could indirectly decrease small mammal food availability. Ungulates can also indirectly impact small mammals through reducing ground vegetation cover, thus increasing predation risk (Keesing, 1998). Small mammals use vegetation cover to protect them from sight of predators. A study on the hunting behaviour of the tawny owl (*Strix aluco*), a small mammal specialist predator, discovered that more vegetation cover caused a reduction in predation success on wood mice (*Apodemus sylvaticus*) (Southern & Lowe, 1968). They also found another small mammal species, the bank vole (*Myodes glareolus*), to be caught in areas that bordered low vegetation cover, indicating that tawny owls depended on the denseness of vegetation for their predation success. Also the predation success of terrestrial predators can be influenced by vegetation structure. A study in Australia measured hunting success by attaching cameras to feral cats (*Felis catus*), a generalist predator of small mammals. They found the prey, including two species of rodents, were four times less likely to be caught in habitat with complex vegetation that included cover from grass and rocks (McGregor et al., 2015). Further, trampling can compact the soil, making it more difficult for small mammals to make and sustain stable burrows. A cattle exclosure study found soil to be less compact inside the exclosure and measured higher small mammal abundance and diversity compared to the area that cattle had access to. They attributed this effect on small mammals to be partly due to the decreasing suitability of building and maintaining stable burrows (Torre et al., 2007). However, wild ungulates do not appear in such high densities in forests and their effect is therefore presumably less than shown in this experiment. Moreover, compacting of the soil is only relevant in areas that have non-rocky soil. Furthermore, wild boars can have a negative effect on small mammals by destroying their burrows while rooting through the ground (Amori et al., 2016). The last indirect effect occurs through the alteration of inter-specific competition (Flowerdew & Ellwood, 2001). Several small mammal species share a common habitat and resources, creating competition over those resources which include food and shelter (Flowerdew et al., 1985). The change in vegetation structure and community brought about by ungulate grazing can favour some species above others, comparatively increasing their fitness and abundance. The disadvantageous species can then decrease solely because of the inter-specific competition.

Ungulates and small mammals have an overlap in diet which can create a direct competition over food. Some small mammal species are herbivorous, eating non-woody material from grasses and dwarf shrubs. Others are granivorous, depending mostly on seeds for their energy intake and still others focus mainly on invertebrates for food (Butet & Delettre, 2011; Hansson, 1971; Saarikko, 1989). Ungulates also feed on herbaceous plants and seeds and wild boars include invertebrates in their diet. Furthermore, several small mammal species store seeds for later usage (Flowerdew et al., 1985). Wild boars scavenge for these caches and may therefore directly compete with these small mammals (Focardi et al., 2000). Lastly, wild boars are known to regularly prey upon rodents (Amori et al., 2016a; Schley & Roper, 2003).

This study focused on the relation between various ungulate species and small mammal abundance; indirectly through the alteration of ground vegetation cover and directly through food competition (Figure 1). The relation between canopy cover and ground vegetation cover, and thus small mammals, was also explored, since canopy cover is a major influence on ground vegetation (Flowerdew & Ellwood, 2001).

The studied forest ecosystem are forests that are more mature (i.e. not open, not clear cuts) occurring in southern Sweden, where the dominating tree species are pine, spruce and birch, but also including a large amount of other deciduous tree species, like pedunculate oak (*Quercus robur*) (Spitzer et al., 2019). In these forests, the already mentioned ungulate species occur, which are moose, red deer, roe deer, fallow deer and wild boars. Moose and roe deer are classified as being more on the browser side of the spectrum, while red deer and fallow deer are classified as mixed-feeders (Hofmann, 1989). Wild boars are omnivorous yet also classify as grazers (Vera, 2000). The small mammal species occurring in this area are wood mice, yellow-necked mice (*Apodemus flavicollis*), bank voles, field voles (*Microtus agrestis*) and common shrews (*Sorex araneus*). Wood mice are generalist and opportunist and can be found in all stages of forest succession. They are considered to be largely granivorous, yet also include invertebrates in their diet. Furthermore, they have well-developed olfactory, auditory and visual senses and considerable agility, enabling them to escape from predators. Yellow-necked mice, also equipped with the senses and agility of the wood mice, are habitat specialist and are known to be more abundant in mature forests with less ground cover, but with dense canopy cover. Like the wood mouse, they feed mostly on seeds and partly on invertebrates. Bank voles are generalist forest animals but have a preference for habitat with dense ground cover. They depend largely on forbs for their diet but also feed on seeds and fruits. Field voles prefer a more open habitat (less forested) with dense ground vegetation cover, preferably grass and forbs since they are folivores (Flowerdew et al., 1985). Furthermore, they can be abundant in clear cuts and reforestation areas, where they can debark tree seedlings and thus, like the ungulates, delay the successional process of the forest. This can also be done by the bank vole, but to a lesser extent (Hansson, 1978). Shrews are habitat generalist, selecting for dense field cover in all stages of forest succession and their diet consist mostly of invertebrates (Flowerdew et al., 1985).

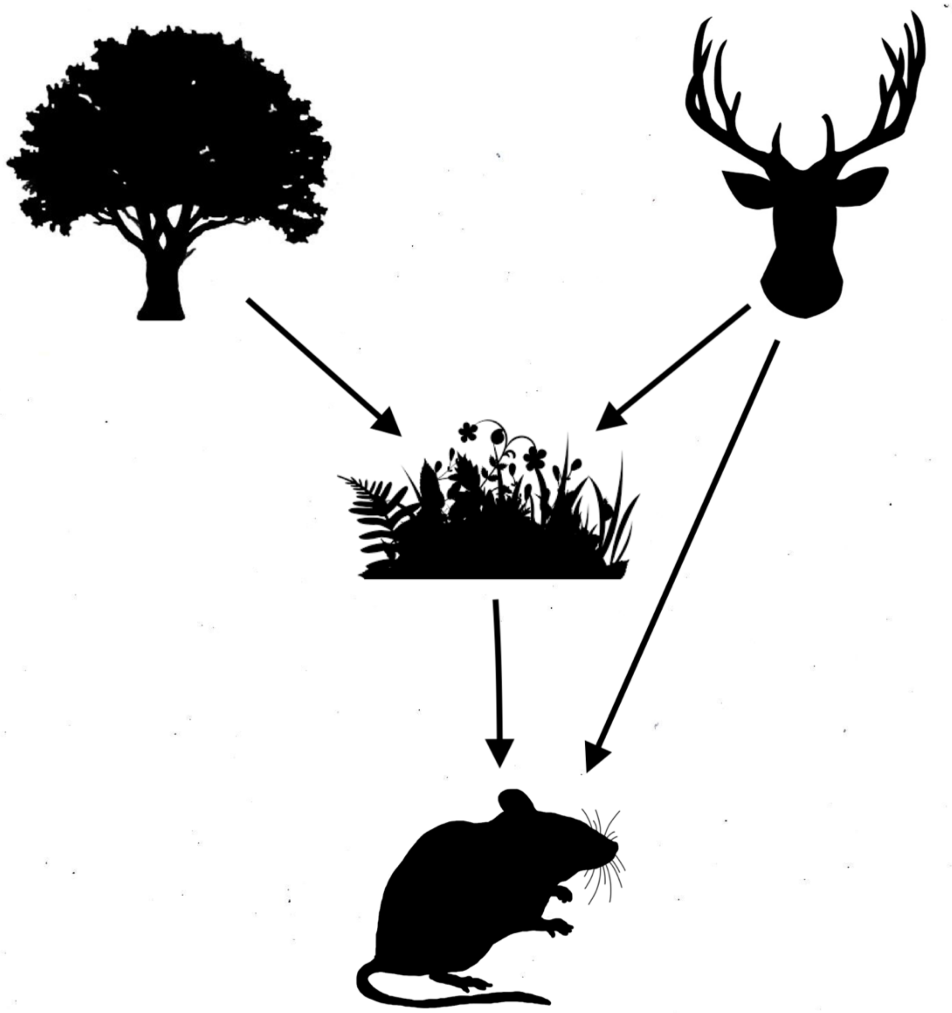

Figure 1. The direct relation between ungulates and small mammals and the indirect relation between canopy cover and small mammals and ungulates and small mammals via ground vegetation.

I hypothesize that ungulates and overall small mammal abundance will be (1) indirectly negatively correlated due to a negative impact of grazing on ground vegetation cover, thus decreasing shelter from predators, and (2) directly negatively correlated through food competition. Further, I predict canopy cover to negatively correlate with ground vegetation cover due to shading from the canopy, consequently negatively correlating canopy cover with small mammals. Moreover, I expect the degree and cause of impact to differ among small mammal species. As previously described, the small mammal species have their preferred habitat and diet and will be correlated to ungulates according to those preferences.

Bank voles will have a strong positive correlation with vegetation cover, since bank voles are diurnal and need dense ground cover to hide from predators (Ecke et al., 2001; Flowerdew et al., 1985). Furthermore, they will be negatively correlated with ungulates because they are both herbivorous. Wood mice and yellow-necked mice will be less correlated with vegetation cover than other small mammals due to their agility and well-developed senses (Buesching et al., 2011; Flowerdew et al., 1985). However, these *Apodemus* species will be directly negatively correlated with ungulates due to their overlap in diet. Field voles prefer dense ground vegetation cover and will therefore be highly correlated with grazing, but since field voles prefer open habitat and the data of this study was gathered in the more mature forests, I expect to catch few field voles. Shrews will be positively correlated with vegetation cover, but not correlated with ungulates directly, since the majority of their diet does not overlap. Lastly, Keesing (1998) suggested that body weight of small mammals decreases with food availability. Therefore, I expect body weight to negatively correlate with ungulate densities.

Additionally, I predict all ungulates to negatively correlate with vegetation cover since ungulates are herbivorous and eat vegetation cover away. However, grazers and browsers will have a different degree of impact on vegetation cover, where grazers will eat grass vegetation cover and browsers woody vegetation cover. Forests will generally contain less grass than woody vegetation; hence I expect the browsers to be more influential in changing the ground vegetation cover. Moreover, wild boars can completely clear areas of vegetation through rooting, thus are expected to decrease vegetation cover dramatically.

Lastly, because the effect of ungulates on vegetation could express itself after several years, I will additionally look at ungulate densities over an eight-year time scale to see if continuous browsing and grazing pressure is correlated to the current ground vegetation cover and small mammal abundance.

2. Methods

2.1. Study area

I performed this study in the area between Gnesta and Nyköping (58°57'07.6"N, 17°09'25.4"E), in the province of Södermanland, Sweden between June and August 2019 (Figure 2). The Beyond Moose research program at SLU (Swedish University of Agricultural Sciences) used this area for several years and established 50 tracts of 1x1 km with four sampling plots on each side, adding up to 16 plots per tract (Figure 3). They conducted Faecal Pellet Group (FPG) counts in April since 2012 for all possible plots of all tracts (i.e. plots that were not located on roads or water).

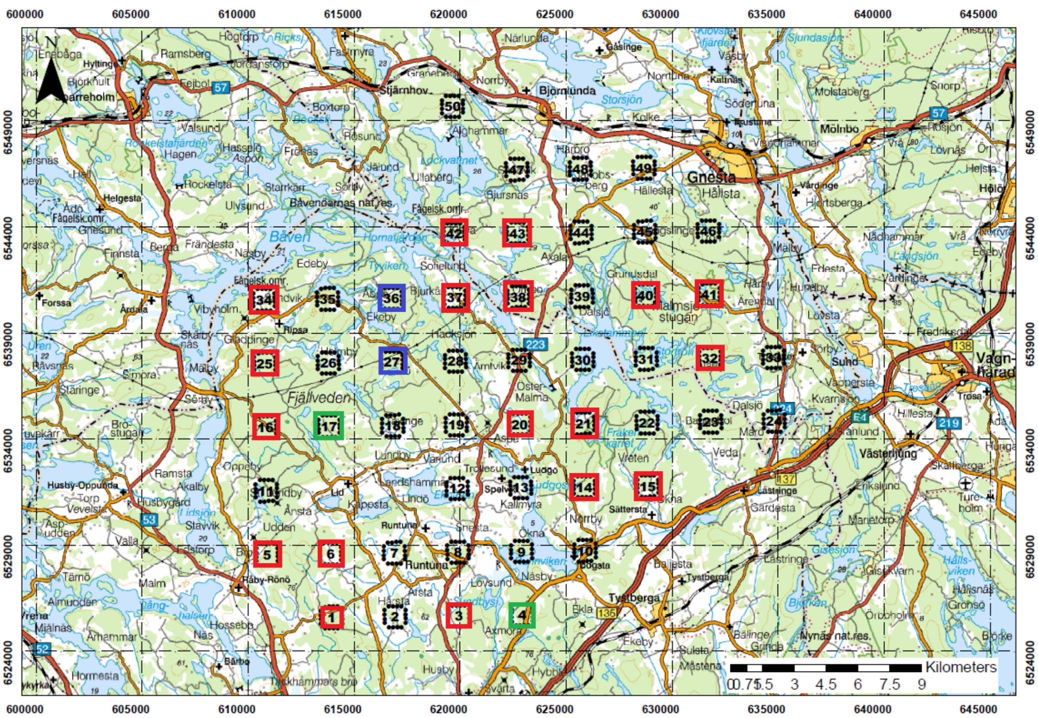

Figure 2. Locations of the 50 tracts in the area between Gnesta and Nyköping. The tracts depicted with a red border are tracts selected and used during the fieldwork. The tracts with a green border were selected, but later replaced with the tracts with a blue border due to problems with permission from landowners.

2.2. Tract and plot selection

For this study, we used 20 of the 50 tracts and eight plots per tract to collect additional data on ungulates, small mammals and vegetation. The selection of these tracts was based on FPG count data from 2016, 2017 and 2018. The average FPG count per tract was calculated for each animal species for those years using the equation (1)

$$\mu_{t_{i_y}} = \frac{\sum_{p=1}^{16} d_{p_{t_{i_y}}}}{16} \tag{1}$$

where $\mu_{t_{i_y}}$ is the average FPG count on tract t for species i in year y and $d_{p_{t_{i_y}}}$ is the dung count on sampling point p on tract t for species i in year y. Then we ranked the tracts where the highest average FPG count got a score of 1 and the lowest a score of 50. The average rank of the tract per species was then calculated using equation (2)

$$r_{i_t} = \frac{\sum_{y=2016}^{2018} k_{i_{t_y}}}{3} \tag{2}$$

where r_{i_t} is the average ranking of species i on tract t and $k_{i_{t_y}}$ is the ranking of species i on tract t in year y. Species on a tract with a rank of 25 or lower were considered to have a high density, and species on a tract with a rank higher than 25 were considered to have a low density. We selected the tracts based on these scores to get an as strong a variation of densities as possible among tracts. For example, we would choose a first tract that had a (1) high, (2) high, (3) low, (4) low, (5) low density and a second tract that had a (1) low, (2) low, (3) high, (4) high, (5), high density for (1) moose, (2) red deer, (3) roe deer, (4) fallow deer, (5) wild boar, respectively. However, we would not select another tract that resembled the densities of one of those already selected tracts.

Two initially selected tracts had to be changed due to problems getting permission from landowners and we replaced those with tracts where the landowners already provided permission and where the ungulate densities did not differ much from the initial tracts (Figure 2).

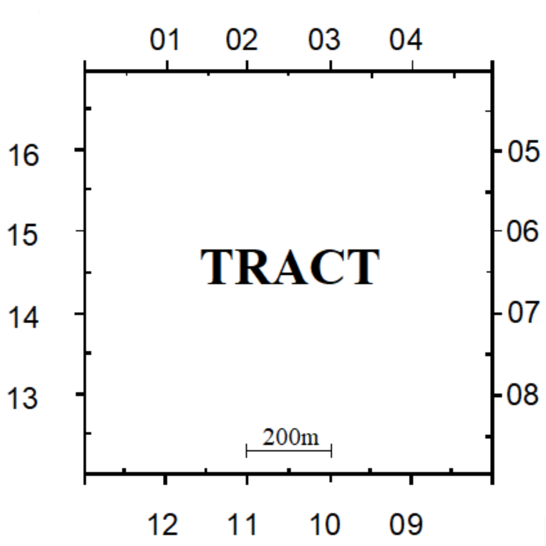

Figure 4. Tract with 16 plots and 200 m between them.

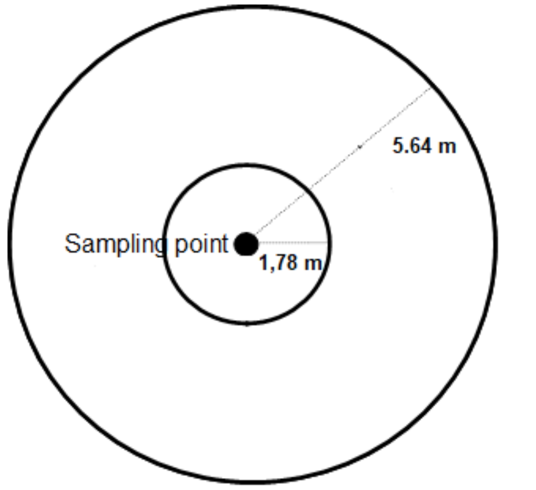

Figure 3. A representation of a plot with a stick in the center which has a rope going outward from it. The rope is marked at 1.78 m and 5.64 m, making a circle of 10m² and 100m² respectively

We selected eight out of the 16 plots per tract with the aim to maximize distance among plots. The plots were given numbers (Figure 3) and we chose to sample the even numbered plots. If a plot was not located in a mature forest (with trees higher than 5 m), it was replaced with a plot on the same side of the initial plot. If there was no suitable plot available on the same side, a plot on the following side (clockwise) was chosen.

2.3. Ungulate density

We estimated relative ungulate densities using FPG counts on the selected plots that we located using a GPS. Subsequently, we put a stick in the ground to mark the center of the plot and tied a rope to the stick. The rope was marked at 1.78 m and 5.64 m which makes a circle of 10 m^2 and 100 m^2, respectively (Figure 4). In the 100 m^2 plot, we counted the FPGs of moose and red deer but only the pellet groups that consisted of at least 20 pellets. We also measured percentage of rooting by wild boar in the 100 m^2 plot by estimating the uprooted ground. In the 10 m^2 plot, FPGs from fallow deer, roe deer and wild boar were included in the measurement, which had to consist of at least 10 pellets. Since fallow deer and roe deer pellets are difficult/impossible to distinguish by eye, it is common practice in Sweden to differentiate them by number of pellets in the pellet group; less than 45 pellets is considered to be from roe deer and more than 45 pellets is considered to be from fallow deer (Spitzer et al., 2019). For all species, FPGs were only counted if the center of the pellet group was inside the plot. Furthermore, I removed the pellets from the plots, because I originally planned to come back and do a second count so I would exactly know the accumulation time of FPGs, which can then be used to estimate absolute densities, but this never happened due to shortage of time.

In addition to my own data, the Beyond Moose project did FPG counts on these locations every year since 2012 till 2019. That data was collected in the same way as described above, expect for three main differences. Firstly, we gathered the data in the summer months of June and July, while the Beyond Moose project conducted their measures the spring month of April. Secondly, I was the only observer for the FPG counts for my data, yet the Beyond Moose project employed 16 different observers over the years to perform FPG counts. And lastly, I spent more time on the plots than the Beyond Moose observers because I removed the pellets from the plots, increasing my detectability of FPGs.

To get the relative densities that are used in the models, I converted the FPG counts of roe deer, fallow deer and wild boar to be over a 100 m^2 area. I summed the FPG counts of all species together to get the relative overall ungulate density per plot. This was used for all models that used the summer 2019 data, except where I investigated the relationship between individual species of ungulate and individual species of small mammals. For that, I used the relative densities of the species per tract, since there was not enough data per species available to model on a plot scale. The relative density per species per tract was calculated by summing the FPG counts of the same species from the same tract. To get the relative densities for 2012 to 2019, I took the average FPG count of the eight years per plot per species. I then also converted this to be over a 100 m^2 area for all species and finally added the species averages together to get a relative overall ungulate density per plot.

Furthermore, absolute densities of ungulates were calculated using the Faecal Standing Crop equation (3)

$$D = \frac{n}{a \cdot t \cdot d} \tag{3}$$

where D is the density of the selected species, n is the number of FPGs, a is the area over which these pellets are counted, t is the time that the pellet groups have been accumulating (since last autumn's leaf fall, which started on average 259 days before the PFG counts) and d is the defecation rate of the selected species, which is 14 for moose (Pfeffer et al., 2018), 20 for red deer (Mitchell, 1984), 20 for roe deer (Pfeffer et al., 2018), 25 for fallow deer (Heinze et al., 2011; Massei & Genov, 1998) and 4 for wild boars (Ferretti et al., 2015).

I calculated the absolute densities the same way for the summer and spring of 2019 by first calculating the densities per tract with equation 3 and then averaging those tracts. This first step, calculating densities per tract instead of per plot, was done to lower the variation of densities. For the spring of 2019 data, the calculation was only done for the tracts that were used for the summer of 2019 data to make the comparison between those years as fair as possible. For the densities of 2012 to 2019, I first summed the FPG counts of the plots from the same tracts for all years, then calculated the densities of the tracts and lastly averaged those tracts. This was also only done on the same tracts used for the summer of 2019 calculation.

2.4. Small mammal abundance

We aimed to estimate relative small mammal densities on the same plots where we performed FPG counts. Out of the 160 plots, this was attained for 113 plots. One plot had to be abandoned because of an upcoming storm and for the remaining 46 plots we did not receive permission from landowners to perform small mammal measurements. These were consequently replaced with plots where no FPG counts were done but where permission was already granted. These 46 plots and the one abandoned plot were not used in models that were on plot scale. To measure relative small mammal densities, we placed six snap traps in a radius of 1 m in all directions around the stick used for the FPG count, or if a stick was not present, a new stick was placed. We put the traps in strategic locations where the small mammals were likely to pass (e.g. near a hole in the ground, next to a fallen log) and baited traps with a piece of apple and Polish wicks (Hörnfeldt, 1994). The traps were set out for three days, being checked every day. If a trap caught a small mammal, it was reset and the small mammal taken to the lab for weighing, species identification and determination of functional group (i.e. adult or juvenile). We collected the traps after the third night, resulting in 18 (3x6) trap nights per sampling point, 144 (18x8) trap nights per tract and thus a total of 2880 (144x20) trap night, minus the one abandoned plot so therefore a total of 2862 trap nights. Snap trapping was approved by the Swedish Board of Agriculture (permit number: A 18-2019).

2.5. Vegetation measurements

All the vegetation measurements were done at the same plots as where the snap traps were set. The center of the plot, which was marked by a stick, was also taken as center for the vegetation measurements. We estimated an area of 5x5 m around this center, which included the 1 m radius for snap traps, and measured the percentage of vegetation that covered the ground. We did this separately for the field layer and umbrella vegetation. The field layer included dwarf shrubs (e.g. bilberry, lingonberry, heather), tree seedlings, grasses, forbs, ferns, lycophytes and horsetails (genus *Equisetum*) below a height of 50 cm. The umbrella vegetation included the same vegetation types as the field layer but with a height between 50 cm to 5 m and excluded non-dwarf shrubs and young trees. Based on their ground cover estimates, they were classified into a five-graded scale which can be seen in Table 1. The class values were then added up to make the ground vegetation cover values that were used in all the models.

Table 1. Five-graded scale for the cover percentage.

Class	Cover-%
1	0
2	>0-12
3	>12-25
4	>25-50
5	>50

Furthermore, we estimated canopy cover on these plots by taking a picture of the canopy with a phone. The picture was taken from breast height, shooting straight up from a position in the plot that represented the overall canopy of the plot best. The photo was then uploaded to the software program ImageJ2 (Rueden et al., 2017). This program converted the picture to black and white, where canopy was black and the sky was white, and calculated the percentage of black in the picture, which was the measure for canopy cover.

2.6. Statistical analysis

Path models can test indirect effects of predictor variables on response variables. In this study, the tested indirect effect was from ungulates on small mammals by altering the habitat. Path models therefore seemed to be the appropriate choice to investigate this relationship. The path models were constructed using the package piecewiseSEM (Lefcheck, 2016) and the package lme4 (Bates et al., 2015) was used to specify mixed effect models with Poisson distribution. All statistical analysis were done in the program R (R version 3.6.1, R Core Team, 2019).

I first created a path model to investigate if overall ungulate density had an effect on ground vegetation cover and subsequently on overall small mammal abundance. Furthermore, the direct effect of the overall ungulate density on the overall small mammal abundance and the effect of canopy cover on ground vegetation cover were included in the model (Table 2, Model 1). Small mammal abundance had a Poisson distribution and a generalized linear model was therefore used. Additionally, the data was hierarchical because plots in the same tract were more similar to each other than plots from different tracts. Therefore, tracts were taken as a random effect.

To analyse the effect of ungulates on small mammals over a longer time period, I repeated the above model structure, but with overall ungulate densities per plot from 2012 to 2019 (Table 2, Model 1).

The next model investigated the effect of individual ungulate species on individual small mammal species. This was done on a tract scale, because there was too little data for individual species to perform reliable analysis on. The path model consisted of four models; one linear model with ground vegetation cover as response variable and moose, red deer, roe deer, fallow deer and wild boar as the predictor variables, and three generalized linear models with Poisson distribution, where the yellow-necked mouse, the bank vole and the wood mouse were the response variables and, for all three models, the ground vegetation cover, moose, red deer, roe deer, fallow deer and wild boar the predictor variables (Table 2, Model 2). Furthermore, only seven plots were snap trapped on one tract and number of plots per tract was therefore used as an offset in the path model. Canopy cover is not taken into this model, because canopy cover does not affect ground vegetation cover on a tract level.

I tested the effect of ungulates on small mammal weight in a path model with the overall ungulate density and canopy cover as predictor variables and ground vegetation cover as a response variable in a linear mixed effect model with tracts as a random variable (Table 2, Model 3). This path model also contained a linear mixed effect model with small mammal weight as response variable and ground vegetation cover and overall ungulate density as predictor variables. The random effects for this model were tract, small mammal species, small mammal sex and small mammal functional group. However, this model did not converge and I therefore transformed the ungulate data for this model, where I added one to all values, to change zeros to ones, and then took the log10 of those values.

The final two models analysed the effect of wild boars on small mammals, but with either FPG count or rooting data as the predictor variable so that the results can be compared. The path model structure created was the same as Model 1 (Table 2), but ungulates was either wild boar FPG count data or wild boar rooting percentage data.

Table 2. Specifications of the three path models. Model 1 investigated the effect of ungulate density and canopy cover on vegetation cover and subsequently on small mammals with also a direct effect of ungulates on small mammals. This model was used for the overall short- and long-term ungulate densities as well as for wild boar and rooting data. Model 2 investigated the individual ungulate species effect on individual small mammal species on tract level. Model 3 investigated the effect of ungulate density on small mammal weight directly and indirectly through vegetation cover and the effect of canopy cover on vegetation cover.

Model 1	psem*(* lmer*(vegetation cover ~ ungulates + canopy cover + (1|Tract)),* glmer*(small mammal abundance ~ vegetation cover + ungulates + (1|Tract), family = poisson(link="log")))*
Model 2	psem*(* lm*(canopy cover ~ moose + red deer + roe deer + fallow deer + wild boar, offset = number of plots per tract),* glm*(Apodemus flavicollis ~ vegetation cover + moose + red deer + roe deer + fallow deer + wild boar, family = poisson(link="log"), offset = number of plots per tract),* glm*(Myodes glareolus ~ vegetation cover + moose + red deer + roe deer + fallow deer + wild boar, family = poisson(link="log"), offset = number of plots per tract),* glm*(Apodemus sylvaticus ~ vegetation cover + moose + red deer + roe deer + fallow deer + wild boar, family = poisson(link="log"), offset = number of plots per tract))*
Model 3	psem*(* lmer*(vegetation cover ~ ungulates + canopy cover + (1|Tract)),* lmer*(small mammal weight ~ vegetation cover + ungulates + (1|Tract) + (1|Species) + (1|Sex) + (1|Functional group)))*

3. Results

3.1. Small mammal abundance

In total, 55 small mammals were caught during the 2862 trap nights. The most abundant species was the yellow-necked mouse, followed by the bank vole and wood mouse. The field vole and common shrew were caught too scarcely to perform reliable analysis on and were therefore left out of the analysis of individual small mammal species. Furthermore, one *Apodemus* species was left unidentified (Table 3).

Table 3. Small mammal species caught over 2862 trap nights.

Species	Common name	Number caught
Apodemus flavicollis	Yellow-necked mouse	24
Myodes glareolus	Bank vole	16
Apodemus sylvaticus	Wood mouse	10
Microtus agrestis	Field vole	1
Sorex araneus	Common shrew	3
Apodemus unidentified		1
Total		55

3.2. Ungulate densities

In total, 642 pellet groups were counted during this study. The most abundant ungulate species in the area was wild boar, followed by roe deer and fallow deer as shown in Table 4. Moose and red deer were comparetavely scarce in the area. The total minimum density is larger than zero even though individual species showed a minimum of zero. This is because there were no tracts where no faecal pellets of at least one ungulate species were present. This is also the case for Table 5.

Table 4. Densities of the ungulate species calculated from the data collected in the summer of 2019. The densities are presented in individuals/km2, with minimum/maximum densities and standard errors.

Species	Density	Min/Max	Std. error
Moose	1.06	0.00/3.94	0.24
Red deer	1.30	0.00/7.48	0.36
Roe deer	21.82	0.00/57.92	3.40
Fallow deer	19.47	1.93/66.20	3.30
Wild boar	32.72	0.00/110.30	6.99
Total	76.37	4.59/189.72	10.82

3.3. Ungulate densities from 2012 to 2019

The densities of the ungulates, which were calculated using the FPG counts collected by the Beyond Moose project, are given in Table 5. The second column of the table show the densities based on the data from the spring of 2019. The densities for all species were at least two times lower than the densities from the summer of 2019, and even five times lower for roe deer. In the fifth column of Table 5, densities were calculated using data from spring 2012 to 2019. Also these densities are at least two times lower than those of the summer of 2019, except for moose.

Table 5. Densities of the ungulate species calculated with data from the spring of 2019 in the second column and ungulate densities from the 2012 till 2019 data in the fifth column. Densities are given in individuals/km2, with minimum/maximum densities and standard errors. Spr '19 stands for spring of 2019 and Spr '12-'19 stands for spring of the years 2012 to 2019.

Species	Density Spr '19	Min/Max	SE	Density Spr'12-'19	Min/Max	SE
Moose	0.50	0.00/1.72	0.12	0.89	0.08/2.62	0.14
Red deer	0.64	0.00/2.51	0.18	0.35	0.00/1.06	0.07
Roe deer	4.03	0.00/16.89	0.82	3.04	1.05/6.78	0.32
Fallow deer	8.98	0.00/22.21	1.40	8.27	0.56/16.62	0.95
Wild boar	14.21	0.00/90.01	5.26	10.65	0.00/40.15	2.20
Total	28.34	5.47/ 103.22	5.98	23.20	5.83/52.07	2.68

3.4. Overall short-term model

In the model that did not distinguish between individual species of ungulates or small mammals, ground vegetation cover decreased with canopy cover (est = -2.80 ± 1.00, $p < 0.01$) and small mammal abundance increased with ground vegetation cover (est = 0.43 ± 0.13, $p < 0.001$). Ungulates did not have any significant correlation with ground vegetation cover nor with small mammal abundance. Table 6 gives an overview and a visualization of the results is given in Figure 5.

Table 6. Results from the overall short-term model with estimates, standardized estimates, standard errors and p-values.

Response	Predictor	Est	Std. est	Std. error	P-value
Vegetation cover	Ungulates	0.0092	0.1635	0.0055	0.1054
Vegetation cover	Canopy cover	-2.7990	-0.2715	1.0035	0.0076**
Small mammals	Vegetation cover	0.4318	-	0.1275	0.0007***
Small mammals	Ungulates	0.0003	-	0.0064	0.9580

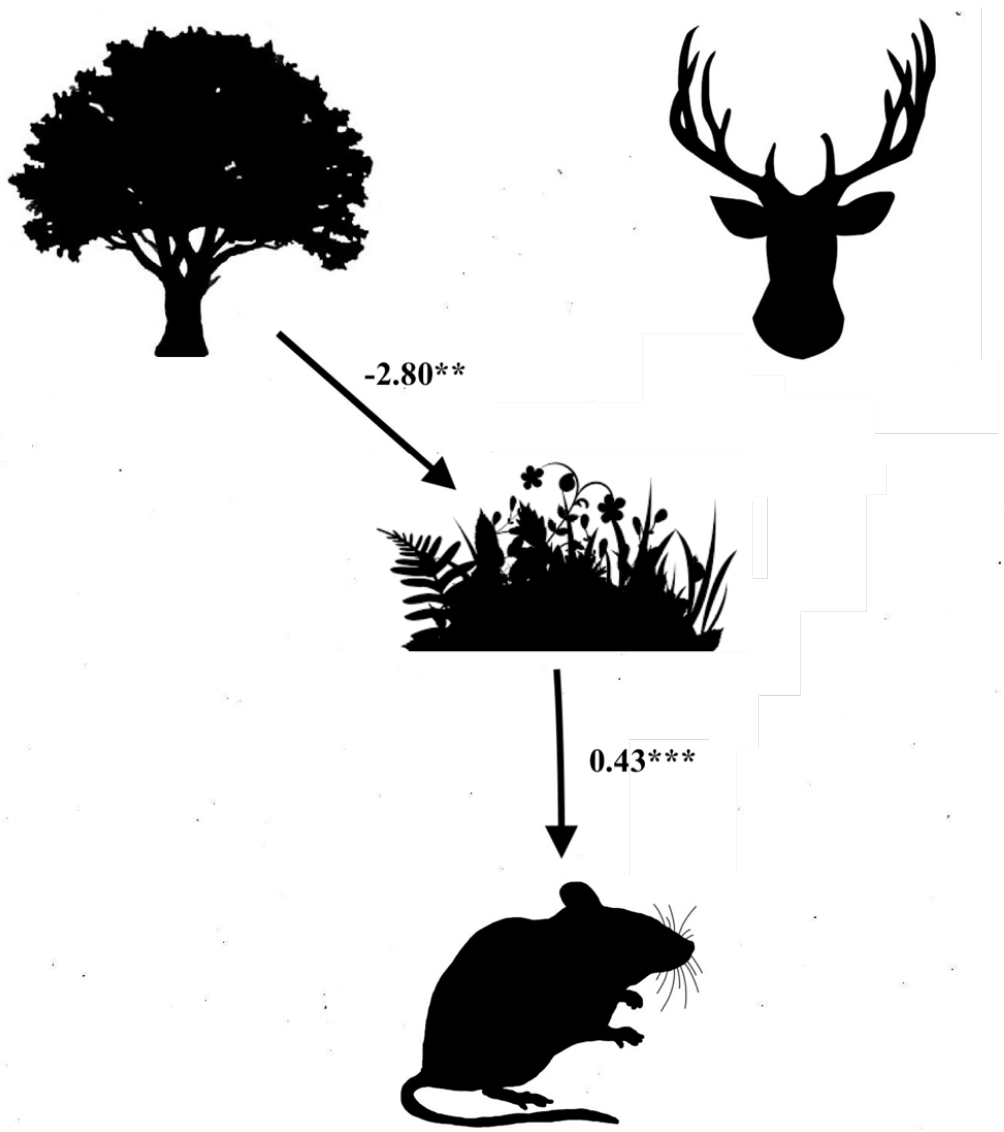

Figure 5. Visualization of the results from the overall short-term model. A correlation between canopy cover and vegetation cover (est = -2.80 ± 1.00, p < 0.01) and a correlation between small vegetation cover and mammal abundance (est = 0.43 ± 0.13, p < 0.001). Ungulate density did not have any significant correlation with vegetation cover nor small mammal abundance.

3.5. Overall long-term model

The model that used FPG count data from 2012 to 2019 had the same results as the overall short-term model, namely that ground vegetation cover decreased with canopy cover (est = -2.33 ± 1.11, $p < 0.05$) and small mammal abundance increased with ground vegetation cover (est = 0.36 ± 0.14, $p < 0.05$) (Table 7). The estimates and p-values are different than those of the overall short-term model (Table 6), because the overlap between the plots used for the 2012 to 2019 FPG count and the plots used for canopy cover, ground vegetation cover and small mammal abundance was lower than the overlap between the plots used for the summer of 2019 FPG count and the plots used to estimate canopy cover, ground vegetation cover and small mammal abundance.

Table 7. Results from the overall long-term model with estimates, standardized estimates, standard errors and p-values.

Response	***Predictor***	***Est***	***Std. est***	***Std. error***	***P-value***
Vegetation cover	Ungulates	0.0128	0.0528	0.0273	0.6499
Vegetation cover	Canopy cover	-2.3330	-0.238	1.1125	0.0470*
Small mammals	Vegetation cover	0.3616	-	0.1444	0.0123*
Small mammals	Ungulates	-0.0152	-	0.0340	0.6537

3.6. Individual species model

The results from the models that tested the correlation between individual species of ungulates and ground vegetation cover and individual small mammal species and between ground vegetation cover and individual small mammals species are given in Table 8. Yellow-necked mouse (*A. flavicollis*) abundance increased with fallow deer (est = 0.09 ± 0.04, $p < 0.05$) and wild boar densities (est = 0.32 ± 0.11, $p < 0.01$). Bank vole (*M.glareolus*) abundance decreased with roe deer densities (est = -0.25 ± 0.10, $p < 0.01$).

Table 8. Results from the individual species model with estimates, standardized estimates, standard errors and p-values.

Response	***Predictor***	***Estimate***	***Std. est***	***Std. error***	***P-value***
A.flavicollis	Vegetation cover	0.0003	-	0.0572	0.9962
M.glareolus	"	-0.1041	-	0.0684	0.1283
A.sylvaticus	"	0.0431	-	0.0787	0.5839
A.flavicollis	Moose	-0.0553	-	0.1274	0.6645
M.glareolus	"	0.1335	-	0.0922	0.1476
A.sylvaticus	"	-0.2657	-	0.2124	0.2108
Vegetation cover	"	0.8574	0.4259	0.5153	0.1183
A.flavicollis	Red deer	-0.0101	-	0.0709	0.8868
M.glareolus	"	-0.0535	-	0.0642	0.4039
A.sylvaticus	"	-0.0262	-	0.0779	0.7369
Vegetation cover	"	-0.1437	-0.1628	0.2142	0.5133
A.flavicollis	Roe deer	-0.0839	-	0.0562	0.1360
M.glareolus	"	-0.2529	-	0.0959	0.0084**
A.sylvaticus	"	-0.0165	-	0.1099	0.8807
Vegetation cover	"	-0.3112	-0.2876	0.3011	0.3190
A.flavicollis	Fallow deer	0.0873	-	0.0444	0.0494*
M.glareolus	"	0.1221	-	0.0839	0.1458
A.sylvaticus	"	0.1289	-	0.0804	0.1089
Vegetation cover	"	0.1766	0.2127	0.2290	0.4534
A.flavicollis	Wild boar	0.3164	-	0.1090	0.0037**
M.glareolus	"	0.1168	-	0.1735	0.5010
A.sylvaticus	"	-0.3941	-	0.2067	0.0566
Vegetation cover	"	0.2470	0.1011	0.6712	0.7183

3.7. Small mammal weight model

Small mammal weight was not significantly correlated with ground vegetation cover nor overall ungulate density (Table 9). In congruence with the results from the overall short-term model in Table 6, this model also shows that ground vegetation cover decreased with canopy cover (est = -3.73 ± 0.99, $p < 0.01$) and that ungulates had no significant correlation with ground vegetation cover.

Table 9. Results of the small mammal weight model with estimates, standardized estimates, standard errors and p-values.

Response	***Predictor***	***Est***	***Std. est***	***Std. error***	***P-value***
Vegetation cover	Ungulates	0.0086	0.0040	0.3124	0.9794
Vegetation cover	Canopy cover	-3.7285	-0.4125	0.9919	0.0016**
Small mammal weight	Vegetation cover	1.1737	0.1691	0.7641	0.2397
Small mammal weight	Ungulates	2.2978	0.1554	1.6985	0.3182

3.8. Wild boar model

Table 10 shows the results from two models, but with different predictor data, namely wild boar FPG counts and wild boar rooting percentages. Small mammal abundance increased with wild boars when the rooting data was used (0.05 ± 0.02, $p < 0.05$), but not when the FPG counts were used ($p > 0.05$). Neither methods for wild boar estimation resulted in a significant relation with ground vegetation cover. Further results, namely the correlation between canopy cover and ground vegetation cover and subsequentually between canopy cover and small mammal abundance, are in congruence with the results from the overall short-term model (Table 6).

Table 10. Results of the two wild boar models with estimates, standardizes estimates, standard errors and p-values. One model used wild boar FPG counts as predictor variable and the other used rooting percentage predictor variable.

Response	***Predictor***	***Est***	***Std. est***	***Std. error***	***P-value***
Vegetation cover	Wild boar dung	0.3209	0.1238	0.2369	0.1858
	Wild boar rooting	-0.0173	-0.0759	0.0213	0.4303
Vegetation cover	Canopy cover	-3.1112	-0.3018	0.9559	0.0022**
	"	-3.2290	-0.3133	0.9651	0.0016**
Small mammals	Vegetation cover	0.4164	-	0.1250	0.0009***
	"	0.5195	-	0.1385	0.0002***
Small mammals	Wild boar dung	0.2958	-	0.2111	0.1612
	Wild boar rooting	0.0498	-	0.0198	0.0119*

4. Discussion

Small mammal abundance was positively correlated with ground vegetation cover, yet the relation between ungulate abundance and vegetation cover was not significant, thus ungulates had no indirect relation with small mammal abundance. Moreover, ungulates and small mammals were not directly correlated. Further, with increasing canopy cover, vegetation cover decreased, suggesting an indirect relation between canopy cover and small mammal abundance through ground vegetation cover.

This study does not provide evidence that vegetation cover decreased with ungulate grazing, which is not what was hypothesised yet is a result that other studies also found (Keesing, 1998; Muñoz et al., 2009). These studies used deer exclosure areas and tested if vegetation cover was different compared to areas where ungulates were present, but no significant difference was found. An explanation for this is a possible shift in plant community, where vegetation does not change in biomass and cover but in species composition (Moser & Witmer, 2000). Another explanation could be that not only ungulates have an impact on vegetation cover, but also vice versa, where ungulates select for areas with high vegetation cover.

The positive relation between vegetation cover and small mammal abundance can be caused by a decrease in predation risk because of more shelter, and by an increase in food availability. It is also possible that small mammals select for patches with dense ground cover because they provide both shelter and food. Interestingly, the significant correlation between vegetation cover and small mammals disappeared at the level of individual small mammal species. Contrasting to these results, a study in Sweden found that bank voles were positively related to umbrella vegetation cover (Ecke et al., 2001) and another study found a correlation between wood mice and total vegetation cover (Abramsky, 1981). The lack of significant effect in our analysis can be caused by several factors. Firstly, the limited number of small mammals that were caught gets emphasized when the small mammal species are modelled individually. Secondly, it is possible that small mammal species have a preferred layer of vegetation cover (e.g. umbrella vegetation, field layer). Species could correlate with the preferred layer, but this would be diluted by analysing the overall vegetation cover, thus making the result insignificant.

It is important to consider that other structural habitat factors than vegetation cover can play a role in small mammal abundance and diversity. Such factors include shrub vegetation, but also factors that are not affected by ungulates such as coarse and fine woody debris and boulders and rocks (Ecke et al., 2002). A study in northern Sweden found grey-sided voles (*Myodes rufocanus*) to be positively correlated with large stone holes which provide shelter (Magnusson et al., 2013). Another study in Sweden found course woody debris to be the most important structural habitat factor for species richness and abundance of bank voles, grey-sided voles, wood lemmings (*Myopus schisticolor*) and common shrews. The logs can provide shelter and food in the form of plants, mosses, lichens and fungi but also can increase the abundance of invertebrates, therefore providing food for insectivorous small mammal species (Ecke et al., 2001). Those factors were not measured in this study but could have played a significant role in small mammal abundance.

Overall ungulate densities did not directly correlate with overall small mammal abundance. A significant effect would have indicated a response of small mammals to direct food competition. But also small mammal body weight did not correlate with overall ungulate densities, additionally indicating that food availability played no role in small mammal fitness (Keesing, 1998). A possible explanation for the lack of significance is that ungulates can have opposing direct impacts on small mammals and therefore cancel each other out. This is what we see when we separate the ungulates and small mammals by species, which show that roe deer were negatively related with bank voles, and wild boars and fallow deer positively related with yellow-necked mice. The negative relation between roe deer and bank voles can be attributed to food competition or, because the test is correlational, to the species selecting for different habitats. The positive relationship of wild boars and fallow deer with yellow-necked mice is opposite of what would be found if the species were competing for food resources but can be explained by those species selecting for the same habitat. Although, it is possible that wild boar rooting exposes a seed bank, making it accessible for the granivorous yellow-necked mouse to feed on this, hence creating a positive relationship.

Another finding of this study is that the two methods for measuring wild boar presence, FPG counts and rooting signs, gave different results for the direct relation with small mammals. FPG counts can be used to measure wild boar density but will say nothing about the behaviour of the animal, while rooting will clearly show where these animals have been disturbing the habitat. The rooting method is therefore better to investigate the effect of wild boar on habitat or where they have been searching for food. In previous papers, it has been suggested that rooting decreased the abundance of small mammals, where bank voles consisted of the majority of the species (Amori et al., 2016), or even completely eliminated the southern red-backed vole (*Clethrionomys gapperi*) and northern short-tailed shrew (*Blarina brevicauda*) from the area (Singer et al., 1984). In a study in Italy, wild boars were actively searching for seeds cached by small mammals, therefore directly competing with the rodents (Focardi et al., 2000). Our results of rooting show a positive direct relation between rooting percentage and small mammal abundance. If wild boars and small mammals were competing for these cached seeds, this would result in a negative relation. However, the Italian study also found wild boar actively excavating small mammal burrows, using them as cues for locating the caches (Focardi et al., 2000). This could lead to an increase in rooting where small mammals are abundant, explaining the positive relation found in this study.

A large obstacle of this study was the low number of small mammals caught in the snap traps. It is possible that the extremely warm and dry summer in the preceding year before our data collection decreased small mammal abundance, since their population dynamic is linked to weather (Batzli & Lesieutre, 1995). Furthermore, vole populations can fluctuate in a three to four year cycle (Hornfeldt, 1994). It is possible that at the time of snap trapping, the population dynamic was at the lower part of the cycle. More small mammal data could have resulted in more significant results and would have been more informative about the field vole and shrew population. Also, because of the multi-annual fluctuations, it is important to measure small mammal abundance over several years. This was not possible and should be considered when interpreting the results. Additionally, the high ungulate densities calculated from the summer 2019 data are unlikely. Compared to the densities calculated from the spring of 2019 data, they are two to five times larger. It is impossible that ungulate population can grow that much in three months. I speculate the difference can be caused by the way I did the FPG counts, where I counted the pellets and removed them from the plots and therefore spent more time on the plots. This increased my detectability for the pellets and therefore higher densities were calculated. This, however, does not change the relative abundance, which was important to analysing this data.

This study contributes to increase our knowledge on the ecology of small mammals, which is important since small mammals have an impact on humans and forest biodiversity. Small mammals function as host for ticks, which can carry pathogens like tick-borne encephalitis virus and *Borrelia burgdorferi* (Jaenson et al., 2012). Increasing understanding of small mammals can help to manage tick populations and thus mitigate transmission of these pathogens. Furthermore, small mammals play an important role in the ecosystem. Specialist predators are highly dependent on them as food source. For example, it was found that when rodent density was extremely low, tawny owls did not even attempt to breed, but when rodent densities rose, a substantial number of owls attempted to breed again (Flowerdew et al., 1985). Another study found that breeding density of Tengmalm's owls (*Aegolius funereus*) was positively correlated with densities of bank voles, field voles and grey-sided voles in autumn and positively correlated to clutch size, number of fledglings per nest and annual production of fledglings with the voles in spring (Hörnfeldt et al., 1990). Biodiversity and abundance of predator species are therefore reliant on small mammal populations.

As can be seen in this study, interactions between organisms can be complex, with indirect and direct effect that sometimes oppose each other. As other papers have found a negative impact of ungulates on small mammals, this was not found in this study. My data does however indicate a negative relation between canopy cover and ground vegetation cover and positive relation between ground vegetation cover and small mammals. Furthermore, when the species were analysed separately, relationships between certain ungulate species and small mammal species became apparent. Future research should take into account other structural habitat factors, since they can have an impact on small mammal abundance and diversity. Furthermore, long-term research should be conducted, where both ungulate densities, habitat factors and small mammal abundance are measured over several years.

References

Abramsky, Z. (1981). Habitat Relationships and Competition in Two Mediterranean Apodemus spp. *Oikos*. https://doi.org/10.2307/3544450

Amori, G., Luiselli, L., Milana, G., & Casula, P. (2016a). Negative effect of the wild boar (Sus scrofa) on the population size of the wood mouse (Apodemus sylvaticus) in forest habitats of Sardinia. *Mammalia*, *80*(4), 463–467. https://doi.org/10.1515/mammalia-2015-0023

Apollonio, M., Andersen, R., & Putman, R. (2010). European Ungulates and Their Management in the 21st Century. *European Ungulates and Their Management in the 21st Century*.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. https://doi.org/10.18637/jss.v067.i01

Batzli, G., & Lesieutre, C. (1995). Community Organization of Arvicoline Rodents in Northern Alaska, *72*(1), 88–98.

Buesching, C. D., Newman, C., Jones, J. T., & Macdonald, D. W. (2011). Testing the effects of deer grazing on two woodland rodents, bankvoles and woodmice. *Basic and Applied Ecology*, *12*(3), 207–214. https://doi.org/10.1016/j.baae.2011.02.007

Butet, A., & Delettre, Y. R. (2011). Diet differentiation between European arvicoline and murine rodents. *Acta Theriologica*, *56*(4), 297–304. https://doi.org/10.1007/s13364-011-0049-6

Cromsigt, J. P. G. M., & Kuijper, D. P. J. (2011). Revisiting the browsing lawn concept: Evolutionary Interactions or pruning herbivores? *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(3), 207–215. https://doi.org/10.1016/j.ppees.2011.04.004

Ecke, F., Löfgren, O., Hörnfeldt, B., Eklund, U., Ericsson, P., & Sörlin, D. (2001). Abundance and diversity of small mammals in relation to structural habitat factors. *Ecological Bulletins*, 165–171.

Ecke, F., Löfgren, O., & Sörlin, D. (2002). Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *Journal of Applied Ecology*, *39*(5), 781–792.

Ferretti, F., Storer, K., Coats, J., & Massei, G. (2015). Temporal and spatial patterns of defecation in wild boar. *Wildlife Society Bulletin*, *39*(1), 65–69. https://doi.org/10.1002/wsb.494

Flowerdew, Gurnell, & Gipps. (1985). The Ecology of Woodland Rodents, Bank Voles and Wood Mice. *The Quarterly Review of Biology*. https://doi.org/10.1086/415465

Flowerdew, J. R., & Ellwood, S. A. (2001). Impacts of woodland deer on small mammal ecology. *Forestry*, *74*(3), 277–287.

https://doi.org/10.1093/forestry/74.3.277
Focardi, S., Capizzi, D., & Monetti, D. (2000). Competition for acorns among wild boar (Sus scrofa) and small mammals in a Mediterranean woodland. *Journal of Zoology*, *250*(3), 329–334. https://doi.org/10.1111/j.1469-7998.2000.tb00777.x
Gill, R. M. A., & Beardall, V. (2001). The impact of deer on woodlands: The effects of browsing and seed dispersal on vegetation structure and composition. *Forestry*, *74*(3), 209–218. https://doi.org/10.1093/forestry/74.3.209
Gill, R. M. A., & Fuller, R. J. (2007). The effects of deer browsing on woodland structure and songbirds in lowland Britain. *Ibis*, *149*(SUPPL. 2), 119–127. https://doi.org/10.1111/j.1474-919X.2007.00731.x
Hansson, L. (1971). Small Rodent Food, Feeding and Population Dynamics: A Comparison between Granivorous and Herbivorous Species in Scandinavia. *Oikos*. https://doi.org/10.2307/3543724
Hansson, L. (1978). *Small mammal abundance in relation to environmental variables in three Swedish forest phases*.
Heinze, E., Boch, S., Fischer, M., Hessenmöller, D., Klenk, B., Müller, J., … Halle, S. (2011). Habitat use of large ungulates in northeastern Germany in relation to forest management. *Forest Ecology and Management*, *261*(2), 288–296. https://doi.org/10.1016/j.foreco.2010.10.022
Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*. https://doi.org/10.1007/BF00378733
Hörnfeldt, B. (1994). Delayed density dependence as a determinant of vole cycles. *Ecology*, *75*(3), 791–806.
Hörnfeldt, B., Carlsson, B.-G., Löfgren, O., & Eklund, U. (1990). Effects of cyclic food supply on breeding performance in Tengmalm's owl (Aegolius funereus). *Canadian Journal of Zoology*, *68*(3), 522–530.
Jaenson, T. G. T., Hjertqvist, M., Bergström, T., & Lundkvist, Å. (2012). Why is tick-borne encephalitis increasing? A review of the key factors causing the increasing incidence of human TBE in Swedena. *Parasites and Vectors*, *5*(1), 1–13. https://doi.org/10.1186/1756-3305-5-184
Keesing, F. (1998). Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia*, *116*(3), 381–389.
Kirby, K. J. (2001). The impact of deer on the ground flora of British broadleaved woodland. *Forestry*, *74*(3), 219–229. https://doi.org/10.1093/forestry/74.3.219
Kuijper, D. P. J., Cromsigt, J., Churski, M., Adam, B., Jędrzejewska, B., & Jędrzejewski, W. (2009). Do ungulates preferentially feed in forest gaps in European temperate forest? *Forest Ecology and Management*, *258*(7), 1528–1535.
Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.12512
Magnusson, M., Bergsten, A., Ecke, F., Bodin, Ö., Bodin, L., & Hörnfeldt, B. (2013). Predicting grey-sided vole occurrence in northern Sweden at multiple spatial scales. *Ecology and Evolution*, *3*(13), 4365–4376.

Massei, G., & Genov, P. V. (1998). Fallow deer (Dama dama) winter defecation rate in a Mediterranean area. *Journal of Zoology*, *245*(2), 209–211. https://doi.org/10.1111/j.1469-7998.1998.tb00089.x
McGregor, H., Legge, S., Jones, M. E., & Johnson, C. N. (2015). Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS ONE*, *10*(8), 1–12. https://doi.org/10.1371/journal.pone.0133915
Mitchell, B. (1984). The defecation frequencies of red deer in different habitats. *Annual Report of the Institute of Terrestrial Ecology*, *1983*, 15–17.
Moser, B. W., & Witmer, G. W. (2000). The effects of elk and cattle foraging on the vegetation, birds, and small mammals of the Bridge Creek Wildlife Area, Oregon. *International Biodeterioration and Biodegradation*, *45*(3–4), 151–157. https://doi.org/10.1016/S0964-8305(00)00036-6
Muñoz, A., Bonal, R., & Díaz, M. (2009). Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. *Basic and Applied Ecology*, *10*(2), 151–160. https://doi.org/10.1016/j.baae.2008.01.003
Parsons, E. W. R., Maron, J. L., & Martin, T. E. (2013). Elk herbivory alters small mammal assemblages in high-elevation drainages. *Journal of Animal Ecology*, *82*(2), 459–467. https://doi.org/10.1111/1365-2656.12009
Pfeffer, S. E., Spitzer, R., Allen, A. M., Hofmeester, T. R., Ericsson, G., Widemo, F., … Cromsigt, J. P. G. M. (2018). Pictures or pellets? Comparing camera trapping and dung counts as methods for estimating population densities of ungulates. *Remote Sensing in Ecology and Conservation*, *4*(2), 173–183. https://doi.org/10.1002/rse2.67
Putman, R. J., Edwards, P. J., Mann, J. C. E., How, R. C., & Hill, S. D. (1989). Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. *Biological Conservation*, *47*(1), 13–32. https://doi.org/10.1016/0006-3207(89)90017-7
R Core Team. (2019). R: A language and environment for statistical computing. *Accessed 1st April 2019*.
Ramirez, J. I., Jansen, P. A., & Poorter, L. (2018). Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: A semi-quantitative review. *Forest Ecology and Management*, *424*(June), 406–419. https://doi.org/10.1016/j.foreco.2018.05.016
Rooney, T. P. (2001). Deer impacts on forest ecosystems: A North American perspective. *Forestry*, *74*(3), 201–208. https://doi.org/10.1093/forestry/74.3.201
Rueden, C. T., Schindelin, J., Hiner, M. C., DeZonia, B. E., Walter, A. E., Arena, E. T., & Eliceiri, K. W. (2017). ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics*. https://doi.org/10.1186/s12859-017-1934-z
Saarikko, J. (1989). Foraging behaviour of shrews. *Annales Zoologici Fennici*.
Schley, L., & Roper, T. J. (2003). Diet of wild boar Sus scrofa in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, *33*(1), 43–56. https://doi.org/10.1046/j.1365-2907.2003.00010.x
Singer, F. J., Swank, W. T., & Clebsch, E. E. C. (1984). Effects of Wild Pig Rooting in a Deciduous Forest. *The Journal of Wildlife Management*. https://doi.org/10.2307/3801179
Smit, R., Bokdam, J., Den Ouden, J., Olff, H., Schot-Opschoor, H., & Schrijvers,

M. (2001). Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology*, *155*(1), 119–127. https://doi.org/10.1023/A:1013239805915

Southern, H. N., & Lowe, V. P. W. (1968). The Pattern of Distribution of Prey and Predation in Tawny Owl Territories. *The Journal of Animal Ecology*. https://doi.org/10.2307/2712

Spitzer, R., Churski, M., Felton, A., Heurich, M., Kuijper, D. P. J., Landman, M., … Cromsigt, J. P. G. M. (2019). Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities. *European Journal of Wildlife Research*, *65*(2). https://doi.org/10.1007/s10344-019-1264-8

Stewart, A. J. A. (2001). The impact of deer on lowland woodland invertebrates: A review of the evidence and priorities for future research. *Forestry*, *74*(3), 259–270. https://doi.org/10.1093/forestry/74.3.259

Torre, I., Díaz, M., Martínez-Padilla, J., Bonal, R., Viñuela, J., & Fargallo, J. A. (2007). Cattle grazing, raptor abundance and small mammal communities in Mediterranean grasslands. *Basic and Applied Ecology*, *8*(6), 565–575. https://doi.org/10.1016/j.baae.2006.09.016

Vera, F. W. M. (2000). *Grazing ecology and forest history.* CABI publishing.

Acknowledgements

I want to thank Joris Cromsigt for helping me make decisions in how to structure, analyse and write this paper and by quickly and thoroughly giving feedback in the writing process. Also a special thanks to Tim Hofmeester, who enormously helped with the analytical part of this study. I want to thank Nannet Fabri for inviting me to join on the field work to collect the data. Lastly, I want to thank my friends in Umeå that made the Master's thesis year a lot of fun.

Latest issue number in our series Examensarbete/Master's thesis

2020:2	Orkidéer och förekomst av död ved i Jämtländska kalkbarrskogar - Orchids and presence of dead wood in calcareous conifer forests in Jämtland Författare: Linnea Edwang Stridbo
2020:3	Movement ecology of ungulate communities – effect of species densities and habitat selection Author: Linda Zetterkvist
2020:4	Luckhuggning med friställning av asp och sälg – påverkan på epifytiska lavar Author: Maria Michold
2020:5	Dietary preferences of Golden eagles (Aquila chrysaetos) in Sweden – A camera trap approach Author: Tomas Melin
2020:6	Slaughter weight in relation to calving date – can area quality compensate for being born late? Author: Sanna-Maja Breiman Wistbacka
2020:7	Downstream migration and survival of Atlantic salmon (Salmosalar L.) kelts and fallbacks when passing a hydropower plant Author: Frans Byström
2020:8	Nocturnal moths use of novel habitats – A case study on a power line in a forest-mire mosaic in boreal Sweden Author: Oskar Lövbom
2020:9	Not everything that glitters is gold: Does linear infrastructure create an ecological trap for Golden Eagles? Author: Michelle Etienne
2020:10	Comparative movement behaviour and habitat selection of semidomestic herbivore: Central-place grazing versus free-range grazing in Reindeer (Rangifer t. tarandus) Author: Muhammad Fawad Sharif
2020:11	How does species density affect activity patterns of three sympatric ungulate species in a Scandinavian boreal forest? Author: Linda Zetterkvist
2020:12	The importance of Ecoparks for saproxylic beetles – A study on general ecological hypotheses in differently managed landscapes Author: Albin Larsson Ekström
2020:13	Restoration strategies in boreal forests – Prescribed burning and gap cutting effects on plant diversity and community composition Author: Clara Espinosa Del Alba
2020:14	Moose movement speed and home range during the rutting season Author: Irene Hjort

The entire list of published numbers can be found at www.slu.se/viltfiskmiljo