Niche differentiation among boreal mammals and birds regarding their roles as endozoochorical seed dispersers

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Master of Science in Natural Resource Management

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Preface

This master thesis was written as a part of my MSc in Natural resource management at the Faculty of Environmental Science and Natural Resource Management, Norwegian University of Life Sciences (NMBU). It has been really interesting to go through the entire process of a research project, with the fieldwork in Sweden as the highlight! Most of all, I would like to thank my supervisor Sam Steyaert for a study design that yielded many results, good guidance, great text feedback and a lot of help with the statistics. I would also thank my co-supervisor Kari Klanderud for good discussions and text feedback. Thanks to Lene and Snorre for commenting the text! The seedlings from the germination trial would not have been alive without the help of Marte, Natalie, Simen, Snorre, Benedicte and Ina, so I wish to thank them as well! Finally, thanks to Camilla Lindberg, Siri Fjellheim and Ola Heide for helping with determining the taxa of graminoids, and the Norwegian Beaver Project for providing beaver scats.

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Abstract

Plant seed dispersal by endozoochory (seed dispersal via the digestive system of animals) is an important process affecting plant species composition in ecosystems. Recent studies in temperate regions have shown that a wide range of animal species disperse plant seeds via endozoochory, and that plant species from many taxa and with different dispersal adaptations are dispersed through endozoochory. The seed dispersal niche of an animal implies its role as seed disperser, where the assemblage of plant species dispersed is an important component. The endozoochorical seed dispersal niches of the animals in the boreal forest are poorly studied, and this study seeks to assess the seed dispersal niches of an assemblage of medium-sized and large boreal forest mammals and birds by quantifying the assemblage of plant species germinating from their scats.

I sampled scats on forest tracks and roads in southcentral Sweden in July and September 2018 and placed the scats in controlled climatic conditions for seed germination. I used generalized linear models to predict the probability of germinating seeds from different species in scats, and the number of emerging seedlings per species per gram dry scat for the different dispersers.

The omnivores (brown bear *Ursus arctos*, red fox *Vulpes vulpes* and pine marten *Martes martes*) and tetraonids (capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix*) dispersed large numbers of viable seeds, while the herbivores (moose *Alces alces*, mountain hare *Lepus timidus* and Eurasian beaver *Castor fiber*) dispersed few viable seeds. *Vaccinium* spp. were the most common dispersed plant taxa. The scats from omnivores contained viable seeds more often compared to the tetraonids, and they dispersed larger numbers of viable seeds per gram dry scat. *Vaccinium myrtillus* was the most common and numerous plant species in scats of all animals except the capercaillie, where the largest proportion of seedlings were graminoids.

For omnivores and tetraonids, the plant species found in scats did to a large degree reflect the diet of the studied animals. The season in which the scats were defecated was an important factor affecting the composition of plant species in scats, and most decisive for the amounts of *V. vitis-idaea* and *V. uliginosum*. These results indicate that several of the medium-sized and large boreal forest vertebrates have the potential to be important seed dispersers. They may thus have an important role in maintaining and moving the distribution of plant species, facilitating sexual reproduction and gene exchange among plant populations and revegetate, for example, disturbed patches. This study underpins the importance of taking animals and the ecosystem services they provide into account in nature conservation and management.

Contents

Introduction

Endozoochory (seed dispersal after ingestion by animals) is an important ecological process, as it can disperse seeds away from the parent population and over long distances (Howe & Smallwood, 1982). This can benefit various aspects of plant life in terms of metapopulation dynamics, maintenance of genetic diversity and colonization of new patches (Cain et al., 2000; Jordano et al., 2011). At least 60% of all plant species are being dispersed by endozoochory, so this is undoubtedly an important process for the ecosystems and the involved plant and animal species (Howe & Miriti, 2000; Wang & Smith et al., 2002; Jordano et al., 2011). The co-existence and co-adaptation of several animal and plant species in an ecosystem creates possibilities for differentiation in seed dispersal niches among the animals (van der Pijl, 1972; McConkey, 2009). The animal species' seed dispersal niche entails its role as seed disperser in an ecosystem and is defined by the assemblage of plant species the animal species disperses and the deposition of the seeds (McConkey, 2009). During the last decades, several studies about endozoochory have been conducted in temperate regions (e.g. Heinken et al., 2002; Wang & Smith, 2002; Eycott et al., 2007; Jaroszewicz et al., 2013; Albert et al., 2015; Picard et al., 2016) but the endozoochorical seed dispersal niches of the large vertebrates in the boreal forest remains poorly studied (but see Willson & Gende, 2004).

The rapid migration of plants after the last glaciation, is an example of the potential of zoochoric dispersal as a factor that affects the plant colonization and composition of an ecosystem (Clark et al., 1998). Insufficient time has passed since the last glaciation for plant species to colonize high latitudes without vertebrates expanding their ranges northwards and bringing seeds with them (Clark et al., 1998; Cain et al., 2000; Vellend et al., 2003). Other examples are the plants' colonization of remote islands and recolonization of disturbed patches. Seeds without apparent adaptations to long-distance dispersal (e.g. plumes) must rely on a vector, often an animal, to colonize patches (Cain et al., 2000; Hanya et al., 2005; Nathan et al., 2008).

A wide range of plant species are being dispersed by endozoochory in temperate regions (e.g. Heinken et al., 2002; Eycott et al., 2007; Jaroszewicz et al., 2013; Albert et al., 2015). Plants carrying fleshy fruits as propagules are adapted to endozoochory, as fleshy fruits attract and are consumed by frugivores and omnivores (van der Pijl, 1972; Janzen, 1984). However, seeds from plants without a fleshy fruit as a reward to omnivores or frugivores can also be dispersed through endozoochory (Janzen, 1984; Albert et al., 2015), as herbivores can unintentionally ingest and thus disperse their seeds when feeding on the plants' foliage. This hypothesis is often

referred to as the "Foliage is the fruit" hypothesis (Janzen, 1984). This hypothesis applies to dry-fruited species, especially graminoids, which are important food for herbivores (Janzen, 1984; Jaroszewicz et al., 2013; Albert et al., 2015). Dry-fruited seeds can also be dispersed by granivores, as some seeds may survive their digestion (Heleno et al., 2011; Orłowski & Czarnecka, 2013; Orłowski et al., 2016).

Plant traits can be adaptations to endozoochorical dispersal by a specific group of animal species (Jordano et al., 2011). It can be beneficial for the plant to adapt to a certain group of dispersers, since different animals may treat and disperse seeds in different manners (Howe & Smallwood, 1982; McConkey, 2009). For some plant species, it can be crucial that their vector brings them to a specific type of patch where they can germinate and establish ("directed dispersal"), while others need to escape the parent population, or benefit from colonizing patches where the species is absent (Howe & Smallwood, 1982; Howe & Miriti, 2000; Wang & Smith, 2002; Jordano et al., 2011), and many other advantages exist (e.g. being dispersed in a faecal envelope can give a growth advantage) (e.g. Traveset, 1998). Even though the benefits for the plants could be many, the plants and animals in Europe show a small degree of specialization in terms of seed dispersal niches (Eycott et al., 2007; Jaroszewicz et al., 2013).

Animals ingest and disperse seeds from a wide range of plant species, and most species that are endozoochorously dispersed, are dispersed by several vertebrate species (Jaroszewicz et al., 2013), although there are exceptions (Cochrane, 2003; Calviño-Cancela et al., 2012). Some plant species are specialists regarding their endozoochorical seed dispersal vector (Cochrane, 2003; Calviño-Cancela et al., 2012), while other species like the common nettle (*Urtica dioica*). are generalists in this respect (Eycott et al., 2007; Steyaert et al., 2009; Jaroszewicz et al., 2013). The specialists are dispersed by few animal species and are thus more vulnerable to human impacts on the size and distribution of their disperser populations compared to the generalists (Cain et al., 2000; Ozinga et al., 2009; Markl et al., 2012). Our knowledge about the seed dispersal niches of various wildlife species is far from complete. Hence, to maintain current vegetation diversity, nature managers need better knowledge about the plant-disperser relationships (Howe & Miriti, 2000; Jordano et al., 2011).

Recent European studies on endozoochory have described the composition of the viable seed load dispersed by several medium-sized and large birds and mammals (Malo & Suárez, 1995; Heinken et al., 2002; Eycott et al., 2007; Jaroszewicz et al., 2013; Orłowski & Czarnecka, 2013; Albert et al., 2015; Picard et al., 2016). Even though the main focus of these studies has not been seed dispersal niches, some niche differentiation seems to occur, especially between

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herbivores and omnivores (Heinken et al., 2002; Jaroszewicz et al., 2013). Frugivorous omnivores (e.g. red fox, marten *Martes* spp. and brown bear) disperse mostly fleshy-fruited plant species (Herrera, 1989; Schaumann & Heinken, 2002; D'hondt et al., 2011; Lalleroni et al., 2017), whereas herbivores (e.g. cervids, lagomorphs and the bison *Bison bonasus*) are important dispersers for herbaceous plants like graminoids and forbs (Malo & Suárez, 1995; Heinken et al., 2002; Pakeman et al., 2002; Mouissie et al., 2005; Eycott et al., 2007; Jaroszewicz et al., 2009; Albert et al., 2015; Picard et al., 2016). The omnivorous wild boar (*Sus scrofa*) disperses fewer viable seeds than the herbivores, but disperses both fleshy- and dry-fruited species (Heinken et al., 2002; Jaroszewicz et al., 2013). Seeds have also been found in faeces from the herbivorous and semi-aquatic Eurasian beaver (Krojerová-Prokešová et al., 2010). Among the herbivores, some seed dispersal niche overlap exists, and some studies have shown that the seed dispersal niches of several herbivores are nested within the seed dispersal niche of red deer (*Cervus elaphus*) (Eycott et al., 2007; Jaroszewicz et al., 2013).

The reason for the observed differences in the assemblage of plant species dispersed seems to be composed of many factors, but is often explained by the diet of the disperser (Malo & Suárez, 1995; Heinken et al., 2002; Eycott et al., 2007; Jaroszewicz et al., 2013; Albert et al., 2015; Picard et al., 2016). The habitat in which the plants grow explains much of the variation in plant species composition of the seed dispersal niche of dispersers (Heinken et al., 2002; Eycott et al., 2007; Jaroszewicz et al., 2013; Albert et al., 2015; Picard et al., 2016). Some suggest that the digestion system is influencing the seed dispersal niche (Eycott et al., 2007, Jaroszewicz et al., 2013), whereas others have shown that plant and seed traits affect which seeds are being dispersed (Heinken et al., 2002; Pakeman et al., 2002; Albert et al., 2015; Picard et al., 2016).

In this study, I investigate the endozoochorical seed dispersal niches of potential seed dispersers in the Eurasian boreal forest. The brown bear, red fox, pine marten, moose, mountain hare, Eurasian beaver, capercaillie and black grouse are the focal dispersers in this study. By collecting scats of the different species and germinating the seeds within these scats, I will identify the plant species dispersed by each potential disperser. Afterwards, I describe the seed dispersal niches of the boreal animals using the assemblage of plant species dispersed. This will allow comparisons of the seed dispersal niches of the different potential dispersers.

I hypothesize that seed dispersal niche differentiation occurs among medium-sized and large animals in the boreal forest. I predict that the herbivores (moose, mountain hare and beaver) will disperse mostly dry-fruited herbaceous species and omnivores (brown bear, red fox and pine marten) fleshy-fruited species in the *Ericaceae* and *Rosaceae* families, and that this

distinction will represent the niche differentiation. The beaver could be a disperser of aquatic plants and terrestrial herbs, but because of its preference for feeding on roots, stems and leaves of aquatic plants (Simonsen, 1973; Haarberg & Rosell, 2006; Krojerová-Prokesová et al., 2010), it will probably disperse less seeds than the hare and the moose. The seed dispersal niches of the capercaillie and the black grouse have to my knowledge not been studied earlier (but see Welch, 1985; Welch et al., 2000 and Orłowski & Czarnecka, 2013 for other tetraonids), and I hypothesize that they will disperse both dry- and fleshy-fruited plants according to their broad summer diet (Pulliainen & Tunkkari, 1991; Starling, 1992; Moss & Picozzi, 1994; Kashevarov & Pozdnyakov, 1997; Summers et al., 2004; Borchtchevski, 2009).

Materials and methods

Study area

The study was conducted in the Dalarna and Gävleborg counties in southcentral Sweden (Fig. 1). The study area is situated at about 61 degrees northern latitude and 15 degrees eastern longitude. The climate here is continental with a mean temperature of about -7 °C in January and 15 °C in June, and rainfall during the growth season ranging from 350 to 450 mm (Swenson et al., 1999) Snow cover typically last 5-6 months, from October-November to April-May (Swenson et al., 1999). The elevation ranges between 200 and 700 meters above sea level (Swenson et al., 1999).

The main land cover type is boreal forest, intersected by clearcuts and logging roads. Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* spp.) are the dominating trees. The most common shrubs in the area are willow (*Salix* spp.), rowan (*Sorbus aucuparia*) and common juniper (*Juniperus communis*) (Swenson et al., 1999). Among the common plants in the ground layer are bilberry (*Vaccinium myrtillus*), lingonberry (*V. vitis-idaea*) and other ericaceous species. (Swenson et al., 1999). The area houses the complete assemblage of medium (e.g. red fox and roe deer *Capreolus capreolus*) and large (e.g. moose) mammals of the boreal forest (including the four large carnivores brown bear, gray wolf *Canis lupus,* Eurasian lynx *Lynx lynx* and wolverine *Gulo gulo*), and has a good population of forest grouse (hazel grouse *Tetrastes bonasia*, black grouse and capercaillie).
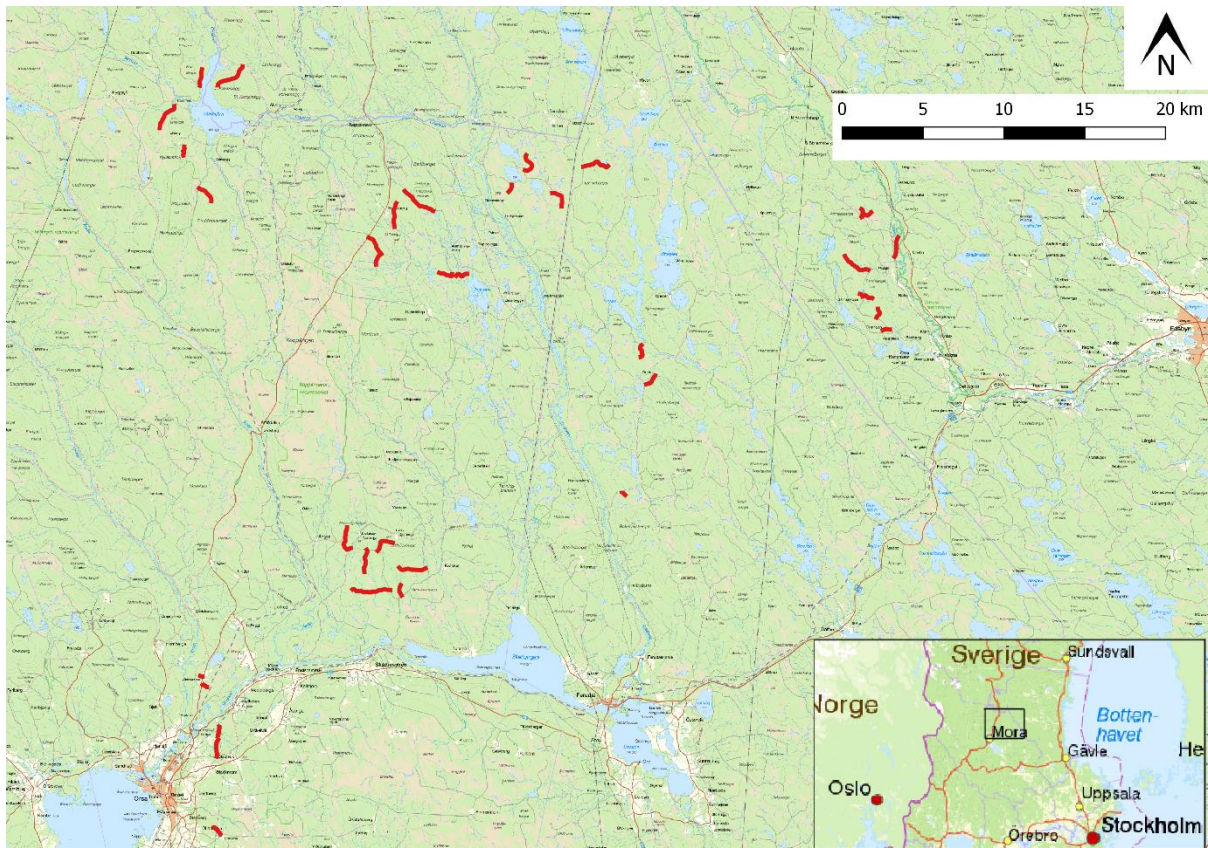
Figure 1. *The study area in southcentral Sweden. The red lines show the 38 forest road and track sections walked when sampling scats. Maps are provided by the WMS service of Lantmäteriet (2019).*

Data collection

The scats were sampled along forest roads, which served as transects. This resulted in efficient sampling, as it was possible to cover longer distances in shorter time compared to walking line transects in forested terrain. In addition, this method allowed for greater detectability of scats compared to detection rates in understory vegetation. Also, repeated sampling along road transects makes it possible to roughly estimate in which period the scat was defecated. It has also been shown that many animals often use and defecate on tracks and forest roads, and that forest roads can act as dispersal corridors for several plant species through endozoochory (Suárez-Esteban et al., 2013).

The selected roads are situated in seven clusters, distributed across the study area (Fig. 1). This stratification increased variation in habitat types surrounding the roads. Because the clusters were spatially separated with at least 4,5 km (i.e. larger than the radius of a standard home range of most forest dwelling medium and large vertebrates), I assumed that the clustering also increased the variation in local animal population densities, and composition of the disperser assemblage. The surroundings of these clusters differed regarding altitude, exposure and human habitation.

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Potential roads and tracks were selected by studying a map, and thereafter included in the study or not, after visual inspection in the field. The main reason for exclusion of potential roads were high numbers of recent driving tracks indicating a current human usage and thus a small probability of detecting intact scats. I selected roads and tracks of different standards, in terms of traffic and use, from gravel roads without vegetation, to paths where the tracks were overgrown and barely visible (Fig. 2). Tracks of all standards were included to increase the diversity of the samples.

Figure 2. Forest road and track sections off several standards were walked when sampling scats in the boreal forest of southcentral Sweden in July and September 2018.

I visited the road segments in May 2018 and removed all the scats on them using a standard broom, to start the sample collection on clean transects. This allowed to add a broad time stamp of defecation on samples collected during subsequent sample collections. By doing this, I could use the season in which the scats were defecated as an explanatory variable for estimating the variation in seed content in the samples. The removal of scats was done by brushing the scats from the roads into the ditches or roadsides. The roads were cleaned from a GPS-marked starting point to the end of the road, or another logical turning point, for example a road split, marked with a GPS-position.

Scats were collected between July 8th and 12th ("summer scats") and between September 16th and 20th 2018 ("autumn scats"). Scats were sampled on 38 cleaned road transects, from the starting point to the end point. The total length of these transects was 41.6 km, they ranged from 171 to 2523 m, and the average sampled road section was 1094 m. The scats were collected in paper bags. Whenever possible, the entire scat was collected. Only a part of the scat was collected if some of the scat was stuck to the ground or smashed. In case of very large scats (e.g. pellet groups from moose), I subsampled 10-20 pellets per scat. In cases where only part of the scat was sampled, I registered the estimated amount of the original scat that was collected. In the field, the outermost layer of the scats was cleaned to remove soil particles and seeds that had been attached to the scat after defecation. Based on experience and literature (Olsen, 2012), the species of animal was recorded for each scat. Also, the GPS-coordinates, the transect identifier and road class were noted, and a picture of the scat was taken.

I received beaver scats from the Norwegian Beaver Project (NBP) in Bø in Telemark, Norway. Beavers are common in the boreal forest of Scandinavia, included the study area (Sveriges Landbruksuniversitet, 2019), but their scats are difficult to find as beavers often defecate in water bodies (Rosell et al., 2001). The NBP collects faecal samples during live captures of beavers (Rosell et al., 2001). Since the beaver scats are collected from a boreal forest resembling the one in the study area, I have chosen to include the beaver scats in the data set. The beaver scats were collected between May 3rd and July 20th 2018.

The scats were weighed and split in two parts. One part was weighed and stored in a freezer prior to dry weight estimation, while the other was weighed and kept for a germination trial. Because of space restrictions in the growth chamber, I randomly selected thirty scats per species and season, in case >30 samples were collected for a given species during one sampling session. The scats from which I was unsure about the identity of the species were discarded.

The part of the scat kept for the germination trial, was gently crushed and put in a labelled pot, on top of a mixture of sterilized sand and seed-free potting soil. Afterwards, they were watered, and put at 4°C for 27 days. This process (cold and wet stratification), can promote germination for certain species (Baskin & Baskin, 1988), and is standard procedure in germination trials (Heinken et al., 2002; Couvreur et al., 2005; Bruun & Poschlod, 2006; Eycott et al., 2007; Picard et al., 2016). The pots with scats were then placed together with control pots (pots with a mixture of sterilized sand and seed-free potting soil) in a closed climate room with controlled climatic conditions, a daylight regime apt for germination trials (12/12 h light dark regime),

ventilation and a temperature that ranged between 21.4°C and 21.8°C. The pots were watered on a daily basis.

The beaver scats were stored cold (4°C) and dark prior to weighing and potting onto soil, which resembles cold stratification as conducted for the other samples.

After germination, I let the seedlings grow until it was possible to identify the species. As soon as identification was possible, I registered the species and removed the seedling. In some cases, I transplanted seedlings in separate pots and allowed them to grow until identification was possible (Muller, 2013). Some seedlings were identified to genus or family level, since species identification would have been too time consuming. Nomenclature off all species complies the Norwegian Biodiversity Information Centre (www.artsdatabanken.no). When the scats had been in the climate room for 90 days, I stopped recording emerging seedlings for this thesis project, as it had a restricted time frame. The germination trial however, continued outside the framework of this thesis. If seedlings emerged from the control pots, an assessment would be needed to decide whether the plant species to which they belonged should be considered as contamination and therefore removed from the dataset.

Because this is a master thesis that had to be delivered within a certain date (May 15th 2019), I was not able to identify the entire seed load in the scats, as some species need considerable time and specific conditions (e.g. frost stratification) to germinate (Baskin & Baskin, 1988). After no more seedlings emerge from the scats after the cold stratification, I will perform a frost stratification, and expose the samples once more to the controlled climatic conditions as described, but that will be outside the framework of this thesis.

The parts of the scats that were not potted, where kept frozen until they were to be dried. The scats were dried in a drying chamber at 60°C for three days. After drying, the scats were weighed. These weights were then used to calculate the dry weight of the parts of the scats that was potted using following equation, and assuming that the water content of the two subsamples per scat was similar.

$$Wp_2 = Wp_1 \times \frac{Wf_2}{Wf_1},$$

[eq. 1]

in which

Wp_2= dry weight of potted scat part,

Wp_1= wet weight of potted scat part,

Wf_2= dry weight of not potted scat part,

Wf_1= wet weight of not potted scat part.

This made it possible to calculate the number of seedlings per gram dry scat (seed load).

$$x = \frac{n}{Wp_2},$$

in which

x = number of seedlings per gram dry scat,

n = number of seedlings counted in a pot.

To show the potential for endozoochorical seed dispersal by an entire population of a seed-dispersing animal species, I calculated the number of viable seeds dispersed by a disperser species per day per square kilometre. This was calculated by using the following equation.

$$y = s * w * b * d,$$

in which

y= the number of viable seeds dispersed by one individual in one day in one square kilometre,
s= number of germinated seeds per gram dry scat,
w= the mean dry weight of a scat from the disperser species in question,
b= the number of scats defecated per day by one individual of the disperser species in question,
d= the population density, given in number of individuals of the disperser species in question per square kilometre.

The used values (b and d) were obtained from scientific articles, books, and published animal population density estimates (Table 3). I chose to calculate these values for the brown bear, red fox, pine marten and joint for the capercaillie and black grouse, as data for these five dispersers were readily available.

Statistical analyses

To perform statistical analyses on plant species with few observations, I grouped several plant species based on their common traits. The groups are 1) plants with fleshy fruits that are not *Vaccinium* spp., 2) graminoids (*Poales*), which here include species from the families *Poaceae, Cyperaceae* and *Juncaceae*, and 3) plants with dry fruits that are not graminoids.

I conducted all statistical analyses using R-Studio in R version 3.5.0. (R core team, 2018). I assessed the seedling emergence probability for dependence of sampling location by fitting a generalized mixed-effects model (GLMM) with "sampling location" (a cluster of road segments) as a random effect. The random effect approached 0 and was thus not informative. Therefore, I chose to use generalized linear models (GLM) to estimate the probability of a scat containing germinating seeds of any species, and to predict the probability of a scat containing germinating seeds from a specific plant or plant group. I fitted the models using a binomial distribution, since seedlings (of a given species) were either being detected as emerging from a scat, or not. When running models predicting the probability of seedling emergence for some plant species or groups, the 95% confidence interval ranged from 0 to 1 for some disperser species, since seedlings emerged from all scats of these dispersers, and thus made the statistical program unable to calculate reasonable confidence intervals. To estimate reasonable confidence intervals, I added one dummy scat with no observations of seedlings emerging to each of the datasets where seedlings emerged from all scats. This was applied to bear scats in both seasons, and to moose scats in summer when estimating values for *V. myrtillus*.

Secondly, I used GLMs to estimate the seed load (number of seedlings emerging per gram dry matter of scat), both for all plant species and for specific plant species or plant groups. Since the seed load data was positive, continuous and the vast majority of the values were concentrated close to zero, I assumed gamma distribution to fit the data. The seed load models included only scats were seedlings of the plant species or group in question were found emerging. Based on the probability of a scat of a specific animal containing germinating seeds of a plant species or group, and its dispersed seed load of the same plant species or plant group, I qualitatively described the seed dispersal niche of the animal.

To select the models to evaluate probability of seedling emergence and seed load, I included the variables disperser species ("species") and sampling period ("season"), and their interaction in the models, and thereafter chose the model with the lowest AICc score (Zuur et al., 2009). I also included a null model in the selection procedure. Models within a ΔAICc (the difference between AICc values of the top ranked models and lower ranked models) range of 2, can also

be considered (Zuur et al., 2009), and in some cases I present results from these models. Based on the GLMs, I performed Tukey pairwise comparison tests to assess differences between dispersers regarding the emergence probabilities or seed loads. This process compared pairs of disperser species and gave an estimated difference, a standard error and a p-value for the difference between them. This was done by using the "glht" function of the R-package "multcomp" (Hothorn et al., 2017). I used an $\alpha = 0.05$ threshold for statistical significance.

To visualize the connections between dispersed plants and dispersers, and the strength of these connections, I made a bipartite graph based on the seed load data. To make the bipartite graph I used the "plotweb" function in the R-package "bipartite" (Dormann et al., 2008). To obtain a value for nestedness, I used the "networklevel" function of the same package (Dormann et al., 2008). A system is nested if groups of species are proper subsets of a larger group of species (Patterson & Atmar, 1986) (here plant species in the seed dispersal niches), and was here measured as "nestedness temperature", ranging from 0 to 100, where lower values are equal to more nested systems (Rodríguez-Gironés & Santamaría, 2006). This metric gives information about the similarity of the seed dispersal niches and can thus be used to assess if there are animals dispersing plant assemblages unique to them.

To assess the diversity of the seed dispersal niches of the different disperses, I calculated diversity of plant taxa in their scats by the Simpson diversity index (Simpson, 1949),

$1 - D$, in which

$$D = \Sigma(\frac{n}{N})^2,$$

in which

D = the diversity index,
n = the total number of organisms of a particular species, and
N = the total number of organisms of all species.

The diversity was calculated using the data on germinated seeds per gram dry scat. This was done using the "diversity" function of the R-package "vegan" (Oksanen, 2007).

Results

Seed dispersal niches of single animal species

I collected a total of 506 scat samples and discarded 22 of those due to species uncertainty. I used 311 scat samples in the germination trial. The number of scat samples used per species varied, between a minimum of 8 (mountain hare) and a maximum of 63 (red fox) (Table 1). Within the framework of the master thesis, the germination experiment lasted from mid-August 2018 to mid-January 2019. Seedlings emerged from 51.8% of the samples (Table 1). The only contamination of the germination trial was one seedling that emerged from a control pot, a graminoid that died before identification of family was possible. Given the rarity of contamination, I decided to ignore potential contamination in the analyses.

Table 1. Summary of the samples used in the germination trial, the proportion of scats with germinating seeds, the average number of seedlings/g dry scat (all scats), the number of plant taxa and the plant species diversity dispersed according to various disperser species. Scat sampling occurred on forest roads and tracks in central Sweden during summer and autumn 2018. Germination trial was conducted in controlled climatic conditions with (12/12 h light dark regime).

Disperser species	Number of scats in trial	Total dry weight of scats (g)	% of scats with seeds germinating	Average number of seedlings per gram dry scat	Number of plant taxa	Plant diversity (Simpson) in scat
Brown bear	13	203.5	100	18.7	9	0.32
Red fox	63	122.4	79	34.4	13	0.53
Pine marten	55	37.3	50	19.5	5	0.39
Moose	37	385.2	3	0.003	1	0.00
Mountain hare	8	22.2	38	0.32	2	0.24
Capercaillie	60	33.2	52	11.7	10	0.65
Black grouse	59	43.9	61	5.88	7	0.53
Eurasian beaver	13	38.6	0	0.00	0	0.00

After excluding seedlings that died before determination of their taxa was possible, 9405 seedlings from 20 plant taxa emerged from the scats (Appendix 1). The dominating taxa among the dispersed plant species were ericoid species (96% of the seedlings), and *Vaccinium myrtillus* being the most abundant (69% of all seedlings) (Fig. 3). *Vaccinium uliginosum* (15%) and *V. vitis-idaea* (12%) were also numerous (Fig. 3). The other most common taxa found were grasses (*Poaceae* spp.), rushes (*Juncus* spp.), sedges (*Carex* spp.), roses (*Rosaceae* spp.) and asters (*Asteraceae* spp.). The red fox dispersed the highest number of plant species (12) and the capercaillie dispersed the most diverse assemblage of plants (Table 1). Despite the relatively high number of seedlings, relatively few species (5) were found in pine marten scats. The seed load ranged from 0 seedlings per gram dry beaver scat to 290 seedlings per gram in the most

seedling-dense red fox scat (Table 1). The probability of detecting seedlings in scats was independent of sampling location, as the variance component of the random effect "sampling location" was 0, according to the mixed effects model.

The network analysis (Fig. 3) and the following calculation of nestedness, revealed that the seed dispersal niches of most animals were similar in terms of species composition, but with differences regarding the relative quantities of the dispersed plant species (Fig. 3). The nestedness temperature was 1.34, indicating a nested system where the plant taxa dispersed by one species to a large degree is a subset of plant taxa dispersed by the other species.
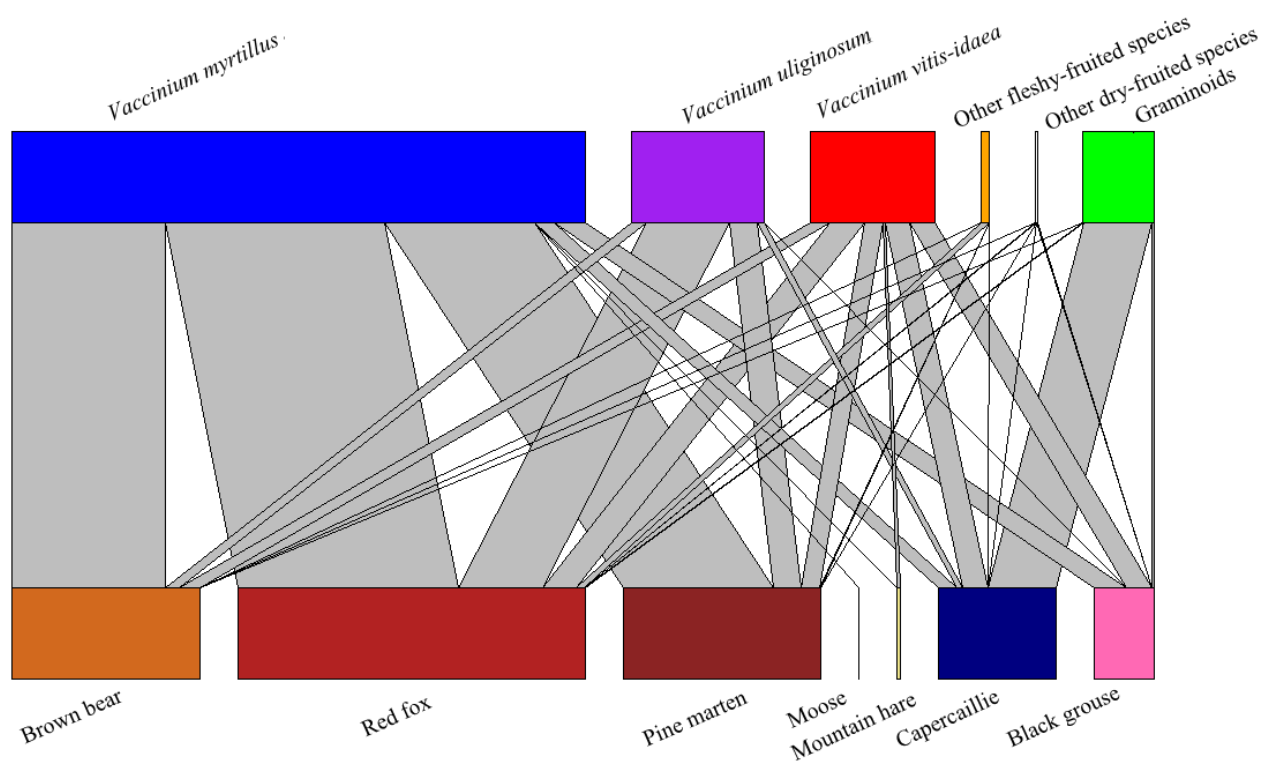

Figure 3. *Seed dispersal relationships between plants and their dispersers in the boreal forest of central Sweden. The width of the connections and the boxes representing species or plant groups, are scaled on basis of the number of seedlings emerged per dry gram scat. Scats were sampled from forest roads and tracks during summer and autumn 2018 and put in controlled climatic conditions for germination trial.*

Of the ten models predicting seedling probability or seed load (Table 2), the best candidate (according to the AIC-criteria) for seven of the models included "species" as an explanatory variable, either alone, additive, or interacting with "season" (Table 2). Three GLMs fitted best with "season" as the only explanatory variable, specifically the detection probability of *Vaccinium uliginosum* and *V. vitis-idaea*, and the seed load of *V. vitis-idaea* (Table 2). The seed load was highest, but most variable in scats from omnivores, and lowest in scats from herbivores (Fig. 4b). The seed load in scats from tetraonids was higher compared to scats from herbivores

but lower compared scats from omnivores (Fig. 4b). The probability of finding seedlings emerging from scats from omnivores and capercaillie was equal or higher in autumn compared to summer, whereas for the black grouse and the moose, seedlings were found emerging from summer scats more often compared to autumn scats (Fig. 4a). For some of the plant species, the season in which the scats were sampled proved to be important for estimating seedling probability and seed load (Fig. 4c). The seed load and seedling probability of *V. vitis-idaea* and the seed load of *V. uliginosum* increased from summer to autumn in scats from all disperser species (Fig. 4c and 6).

Table 2. GLM models with ΔAIC scores <2 to estimate the probability or seed load of different plant taxa germinating under controlled climatic conditions from scats collected in southcentral Sweden summer and autumn 2018. Df = degrees of freedom of the respective candidate model.

Model	Explanatory variables	Df	AIC	Δ AIC
Seedling probability, all plant species	Species*Season	13	343.1	0.00
	Species+Season	8	344.4	1.26
	Species	7	344.6	1.53
Seed load, all plant species	Species*Season	13	1334.8	0.00
	Species	8	1336.5	1.66
Seedling probability, *V. myrtillus*	Species+Season	8	178.9	0.00
Seed load, *V. myrtillus*	Species	8	832.2	0.00
	Species+Season	9	833.3	1.12
Seedling probability, *V. uliginosum*	Species*Season	12	135.9	0.00
Seed load, *V. uliginosum*	Season	3	238.0	0.00
Seedling probability, *V. vitis-idaea*	Season	2	200.6	0.00
	Species+Season	8	200.9	0.31
Seed load, *V. vitis-idaea*	Season	3	470.9	0.00
Seedling probability, graminoids	Species	7	134.4	0.00
	Species+Season	8	135.4	0.92
Seed load, graminoids	Species	5	139.7	0.00
	Species*Season	8	140.4	0.71

The predicted probability of finding seedlings emerging from brown bear scat was high (87% for both seasons) (Fig. 4a), and the predicted seed load dispersed by brown bear was 17.4 seedlings/g dry scat in summer and 27.6 seedlings/g dry scat in autumn, albeit with much variation (Fig. 4b). The seedlings most commonly found emerging from bear scat were *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea* (Fig. 3). *Vaccinium myrtillus* was by far the most common (Fig. 3) and together with *V. uliginosum* they were the most numerous species where they appeared (Fig. 5b). The probability and seed load of *V. myrtillus* remained relatively stable from summer to autumn (Fig. 5). *Vaccinium vitis-idaea* was only found in bear scats from autumn. Less common than *Vaccinium* species were other fleshy-fruited species, like apple (*Malus domestica)*, crowberry (*Empetrum nigrum*) and cranberry (*Oxycoccus* sp.) (Fig. 3). Greater plantain (*Plantago major*) and graminoids were also detected (Fig. 3).
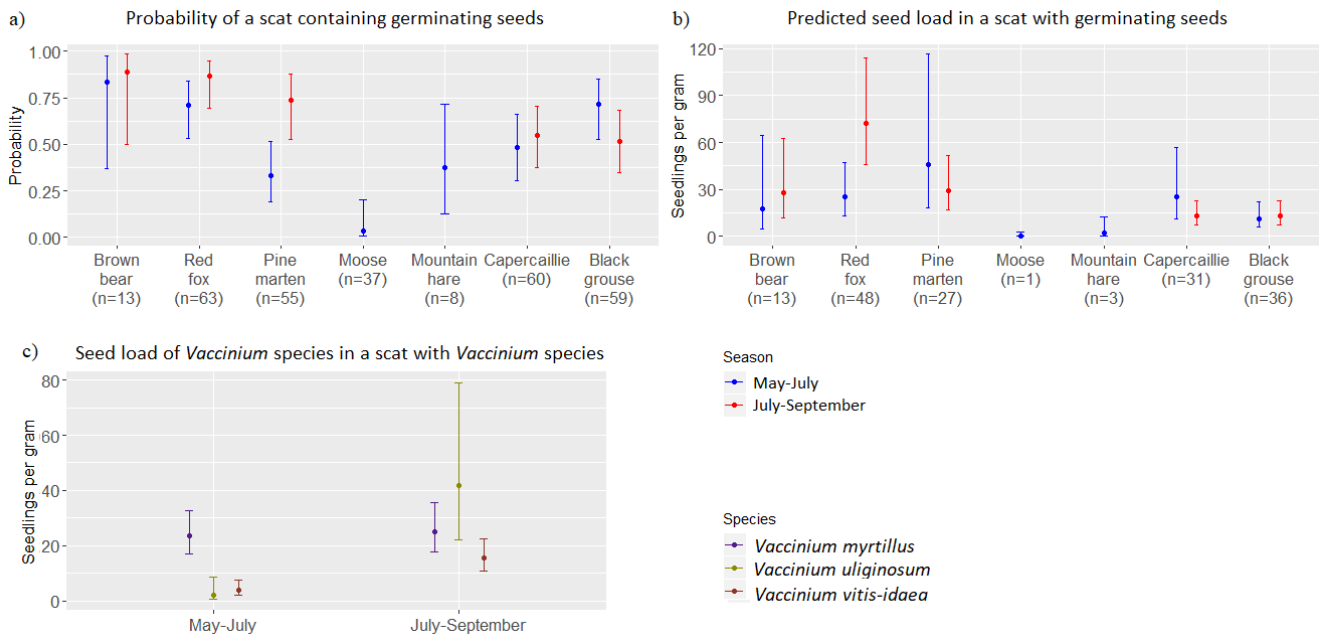
Figure 4. *Results from the germination trial under controlled climatic conditions of seeds in scats collected on tracks and roads in the boreal forest of southcentral Sweden summer and autumn 2018. The predicted probability of germination of at least one seed of any plant species, by a binomial fitted GLM with seedling emergence as response and species and season as interacting variables (a). The predicted seed load of all plant species in a scat, by a gamma fitted GLM with seed load as response and species and season as interacting variables (b). The predicted seed load of Vaccinium species for all dispersers in different seasons, by a gamma fitted GLM with seed load as response and season as explanatory variable (c). For each panel, the error bars indicate 95% confidence interval. (n=x) indicates the number of scats used in the germination trial (a) or the number of scats where seedlings germinated (b).*

The probability of detecting seedlings emerging from pine marten scats was predicted to be 33% in summer and 74% in autumn (Fig. 4a). The seed load dispersed by pine marten was among the highest observed (46.0 seedlings/g dry scat in summer and 29.5 seedlings/g dry scat in autumn) (Fig. 4b). *Vaccinium myrtillus* was by far the most common species emerging from pine marten scat (Fig. 3 and 5a), and other species detected more than once were *V. vitis-idaea* and *V. uliginosum* (autumn only). The probability of finding *V. myrtillus* was similar in both seasons (Fig. 5a). In samples where *V. myrtillus* and *V. uliginosum* appeared, they were numerous (*V. myrtillus* 33.4 seedlings/g dry scat and *V. uliginosum* 28.0 seedlings/g dry scat) (Fig. 5b). *Oxycoccus* sp. and common groundsel (*Senecio vulgaris*) were detected in one scat each (Fig. 3).
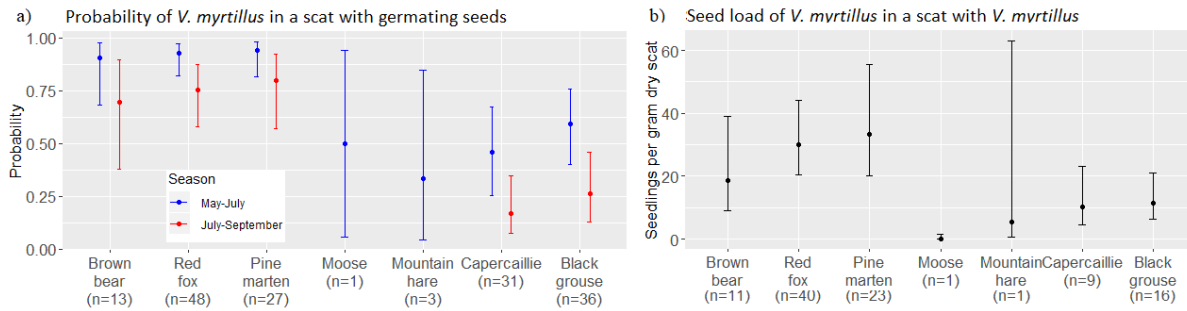
Figure 5. Results from the germination trial under controlled climatic conditions of V. myrtillus seeds in scats collected on tracks and roads in the boreal forest of central Sweden summer and autumn 2018. The predicted probability of a scat from a specific disperser containing germinating V. myrtillus seeds, by a binomial fitted GLM with seedling emergence as response variable and species and season as additive explanatory variables (a). The predicted seed load of V. myrtillus in scats by a gamma fitted GLM with seed load as response and species as explanatory variable (b). Error bars indicate 95% confidence interval. (n=x) indicates the number of scats where seedlings emerged (a) or with V. myrtillus germinating (b).

The predicted probability of detecting seedlings emerging from red fox scats was among the highest (71% in summer and 87% in autumn) of all assessed dispersers (Fig. 4a). The predicted seed load in the scats was higher in autumn compared to summer. In fact, the predicted seed load was the highest among all disperser species (72.2 seedlings/g dry scat) in this study. By far the most probable species to detect was *Vaccinium myrtillus* (predicted detection probability of 86% and 81% in summer and autumn scats, respectively) (Fig. 5a and 3), with a general high seed load (Fig. 5b). *Vaccinium uliginosum* did only emerge from scats collected in autumn. *Vaccinium uliginosum* and *V. vitis-idaea* emerged less frequently than *V. myrtillus,* but *V. uliginosum* was more numerous when it did (Fig. 5 and 6). The assemblage of plants dispersed by the red fox was relatively diverse (Fig. 3, Table 1). Seeds of plants with fleshy fruits other than *Vaccinium* spp., like wild strawberry (*Fragaria vesca*) and *Oxycoccus* sp. were detected in red fox scat, alongside rushes*,* grasses, dry-fruited ground-layer plants (here pearlwort *Sagina* sp. and heather *Calluna vulgaris*), and downy birch (*Betula pubescens)*.
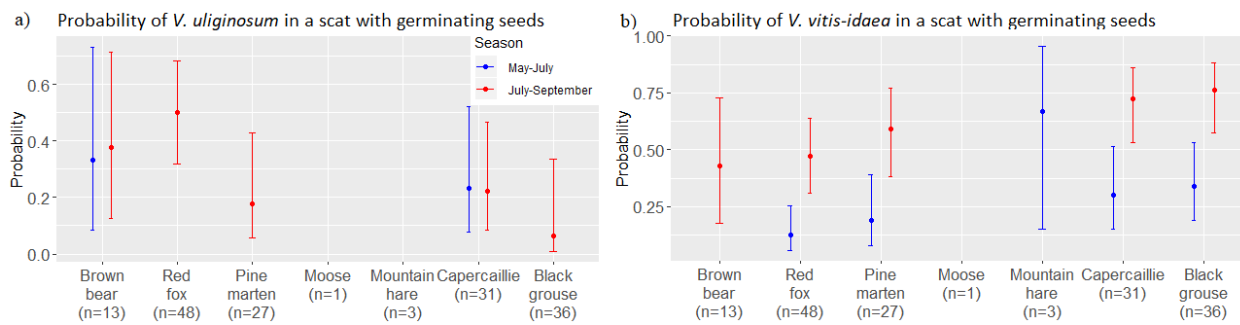
Figure 6. Results from the germination trial under controlled climatic conditions of V. uliginosum and V. vitis-idaea seeds in scats collected on tracks and roads in the boreal forest of southcentral Sweden summer and autumn 2018. The predicted probability of a scat containing germinating seeds of V. uliginosum by a binomial fitted GLM with seedling emergence as response and species interacting with season as explanatory variables (a) and V. vitis-idaea by a binomial fitted GLM with seedling emergence as response and species and season as additive explanatory variables (b). Error bars indicate 95% confidence interval, and (n=x) indicates the number of scats where seedlings emerged.

The probability of detecting seedlings emerging from capercaillie scats was similar in both seasons with an overall predicted probability of 52% (Fig. 4a). The predicted seed load dispersed by capercaillie was higher during summer (25.2 seedlings/g dry scat) compared to autumn (13.2 seedlings/g dry scat) (Fig. 4b). In capercaillie scats, the dominant plant group in terms of seed load was graminoids (22.2 seedlings/g dry scat) (Fig. 4b and 7b), and the probability of a scat with emerging graminoid seedlings was 35% (Fig. 7a). *Vaccinium* species were also common (Fig. 3). The predicted probability of *V. myrtillus* was higher in summer compared to autumn (Fig. 5a). For capercaillie, the probability of detecting *V. vitis-idaea* was higher compared to that of *V. myrtillus* (Fig. 5a and 6b). The probability of detecting *V. uliginosum* seedlings remained stable throughout the sampling period (Fig. 6a). *Oxycoccus* sp. and dry-fruited ground-layer species (greater plantain and woodland arctic cudweed *Omalotheca sylvatica*) were also sporadically detected (Fig. 3).

The probability of detecting seedlings emerging from black grouse scat was predicted to be higher in summer (71%) compared to autumn (52%) (Fig. 4a). The seed load dispersed by black grouse remained stable with an overall mean of 12.0 seedlings/g dry scat (Fig. 4b). The two most common species emerging from black grouse scats were *V. myrtillus*, and *V. vitis-idaea* (Fig. 3), and the probability and seed load for the two species were similar (Fig. 3). The predicted probability and seed load of *V. myrtillus* decreased during the sampling periods (Fig. 5a). One *V. uliginosum* seedling was found in one autumn scat. Graminoids were found regularly (Fig. 7a), with rushes being the most common taxa. The graminoid seed load was low (Fig. 7b). Marsh cudweed (*Gnaphalium uliginosum*) was found in one scat.
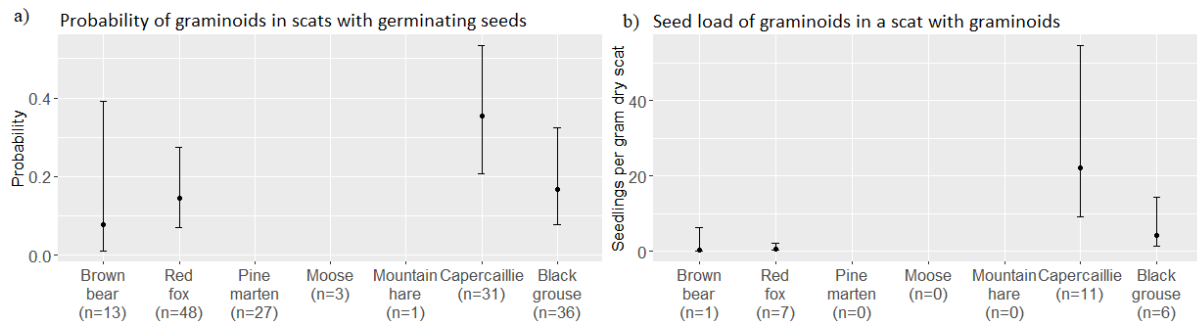
Figure 7. *Results from the germination trial under controlled climatic conditions of graminoid seeds in scats collected on tracks and roads in the boreal forest of southcentral Sweden summer and autumn 2018. Predicted probability of a scat containing germinating graminoid seeds, by a binomial fitted GLM with seedling emergence as response and species as explanatory variable (a). Predicted seed load of graminoid seeds in scats where graminoids were found, by a gamma fitted GLM with seed load as response and species as explanatory variable (b). Error bars indicate 95% confidence interval, and (n=x) indicate the number of scats where seeds germinated (a) or the number of scats where graminoid seeds germinated (b).*

The predicted seed load in scats from the herbivores was low (Fig. 4b), and all comprised *Vaccinium* species (Fig. 3). The probability of finding seedlings emerging from moose scats was low, 3% in summer and 0% in autumn (Fig. 4a). Only one seedling (*V. myrtillus*) was detected in 37 samples totalling 384 g dry scat. The probability of finding seedlings emerging from mountain hare scat was predicted to be 38%, but the 95% CI was large (Fig. 4a). No seedlings were found emerging from beaver scat.

Seed dispersal at the disperser assemblage level

The following results are derived from Tukey pairwise comparison tests based on some of the selected GLMs (Table 2). All results from the Tukey tests used in this text are presented in the supplementary tables of Appendix 2-10. Here, I only present the comparisons with significant differences between seed dispersers.

Using a model with "species" as the only explanatory variable (Appendix 2), the red fox had a significantly higher probability of dispersing germinating seeds compared to both the pine marten (β =1.27, SE=0.42, p=0.030) and the capercaillie (β =1.24, SE=0.41, p=0.030). Using a model with "species" as the only explanatory variable (Appendix 3), the seed load dispersed by red fox was significantly higher compared to capercaillie (β =-1.02, SE=0.31, p=0.014) and black grouse (β =-1.44, SE=0.30, p<0.001). Pine marten dispersed a significantly higher seed load compared to black grouse (β =-1.09, SE=0.34, p=0.021) (Appendix 3).

The probability of detecting seedlings emerging from moose scat was significantly lower compared to scat from brown bear (β =5.46, SE=1.27, p<0.001), red fox (β =4.89, SE=1.06, p<0.001), pine marten (β =3.62, SE=1.05, p=0.009), capercaillie (β =3.65, SE=1.05, p=0.007) and black grouse (β =4.03, SE=1.05, p=0.002) (Appendix 2). The moose dispersed a

significantly lower seed load compared to brown bear (β =5.11, SE=1.40, p=0.004), red fox (β =-5.87, SE=1.37, p<0.001), pine marten (β =5.52, SE=1.38, p<0.001), capercaillie (β =4.85, SE=1.37, p=0.006) and black grouse (β =4.43, SE=1.37, p=0.016) (Appendix 3).

Using an additive model with "species" and "season" as explanatory variables, *V. myrtillus* seedlings were more probable to be found emerging from scats from omnivores compared to capercaillie scat (brown bear: β=2.42, SE=0.80, p=0.036, red fox: β=-2.71, SE=0.59, p<0.001 and pine marten: β=-2.96, SE=0.71, p<0.001) (Appendix 4). With the same model, the black grouse was less probable to disperse seeds compared to red fox (β=-2.17, SE= 0.56, p=0.002) and pine marten (β=-2.42, SE=0.68, p=0.006). The black grouse dispersed also a significantly lower *V. myrtillus* seed load compared to red fox (β=-1.14, SE=0.37, p=0.027) and the pine marten (β=-1.19, SE=0.41, p=0.045) when using an additive model with "species" and "season" as explanatory variables (Appendix 5).

The seed load of graminoids was significantly higher in scats from capercaillie compared to scats from red fox (β =3.52, SE=0.74, p<0.001) and brown bear (β =-4.27, SE=1.59, p=0.033) (Appendix 10). No graminoid seedlings emerged from pine marten, moose or mountain hare scats.

Based on results from this study and other studies, it was possible to estimate the number of seeds dispersed by all individuals of a disperser species in an area (Table 3). At population densities found in Scandinavia, the brown bear, red fox, pine marten and the tetraonids can disperse more than 2400 seeds per day per km^2.

Table 3: *Values used to calculate the number of seeds dispersed by several endozoochorical dispersers per day in 1 km^2 in the boreal forest of Sweden. Here, scats without emerging seedlings are included in the calculation of the number of seedlings per gram dry scat. Small numbers indicate source. 1) Roth (1980), 2) Webbon et al. (2004), 3) Balharry (1993), 4) Estimated from Baltić et al. (2005), 5) Dahle & Swenson (2003), 6) Brainerd (1997), 7) Hjeljord (2008), p. 212, 8) Statskog (2018).*

	Number of seedlings per gram dry scat	Mean dry scat weight (g)	Scats defecated per individual per day		Number of individuals per km^2		Number of seeds deposited per km^2 per day
Brown bear	18.7	69.6	4	[1]	0.02	[5]	104.1
Red fox	34.4	3.9	8	[2]	0.3	[6]	322.0
Pine marten	19.5	1.2	10	[3]	0.3	[7]	70.2
Tetraonids	8.8	1.3	17	[4]	10	[8]	1944.8
Sum							2441.1

Discussion

The seed dispersal niches of the studied dispersers

Overall, only a fraction of the available plant species of the boreal forest were endozoochorously dispersed by the animal species included in this study. The most common and numerous dispersed plant species in the boreal forest of Sweden was bilberry (*Vaccinium myrtillus*). Lingonberry (*V. vitis-idaea*) and bog whortleberry (*V. uliginosum*) were also often dispersed. As hypothesized, the omnivores dispersed mostly fleshy-fruited ericoid species and the tetraonids dispersed seeds from fleshy-fruited and dry-fruited species more evenly in number. Contrary to the hypothesis, the herbivores dispersed few viable seeds from few species, and no viable seeds from dry-fruited plants.

Seedlings emerged from all scats from brown bear, and the probability for dispersing viable seeds was highest for the brown bear among the studied dispersers. The seed load varied greatly among bear scats, and relatively few species germinated considering the amount of bear scat found. *Vaccinium myrtillus* and other *Vaccinium* species were the most common and numerous dispersed plant species, conform with other studies on seed dispersal by brown bear, supporting the perception that the brown bear is an important disperser for *Vaccinium* species (Willson & Gende, 2004; Lalleroni et al., 2017). The brown bear is known to consume large amounts of *Vaccinium* fruits, both in spring and autumn (Elgmork & Kaasa, 1992; Persson et al., 2001; Stenset et al., 2016). *Rubus* and *Ribes* species were common in other studies (Willson & Gende, 2004; Lalleroni et al., 2017) but were not found here. *Malus* spp. seeds were found both here (in low number) as well as in Lalleroni et al. (2017).

As for the brown bear, the largest part of the pine marten's seed dispersal niche was constituted by *V. myrtillus.* The pine marten seemed to be a more specialized *Vaccinium* disperser compared to the other animals studied, as only two non-*Vaccinium* seedlings were found. The pine marten is mainly a predator, but it eats berries in late summer and autumn (Jędrzejewski et al., 1993). This may explain the lower probability of detecting seedlings emerging from summer scats compared to autumn scats, and the virtual absence of seedlings from plants without fleshy fruits. The high amounts of viable *V. myrtillus* seeds in their faeces is in accordance with Schaumann & Heinken (2002), who also reported that seeds of *Rubus* species were abundant in the faeces of pine martens, a taxon that was not detected in this study.

Since fleshy-fruited species, and *V. myrtillus* in particular, constituted the largest part of the seed dispersal niche of the red fox, it resembled the ones of the brown bear and the pine marten.

However, the seed dispersal niche of the red fox seemed to be more diverse compared to the niches of the other omnivores studied, as it was more probable to detect seedlings of non-*Vaccinium* fleshy-fruited species, graminoids and other dry-fruited plants emerging from red fox scats. The probability of detecting seedlings emerging from red fox scat and the seed load dispersed by red fox was high, with relatively little variation. Overall, the red fox dispersed a relatively large number of plant species, which probably reflects its opportunistic feeding behaviour and broad habitat use (D'hondt et al., 2011). The red fox seems to eat and disperse whichever available fleshy fruit (D'hondt et al., 2011). The omnivores dispersed more often and larger numbers of viable *V. myrtillus* seeds compared to the tetraonids, probably because of a higher seed intake (Bruun & Poschlod, 2006), and because of the destructive digestion system of the tetraonids (Welch et al., 2000; Orłowski & Czarnecka, 2009). More seeds should survive ingestion by omnivores, as their teeth are unlikely to destroy seeds (Otani, 2002) and their digestive system is short and simple (Hume, 2002).

Graminoids, *V. vitis-idaea* and *V. myrtillus* were in descending order, the three most common and numerous taxa in the seed dispersal niche of the capercaillie. The seed dispersal niche of the capercaillie was the only dispersal niche studied where another plant group than *Vaccinium* constituted a major part, so the capercaillie seed dispersal niche differed from those of the other dispersers. The seed dispersal niche of the black grouse resembled the omnivore's seed dispersal niche because *Vaccinium* species were the most common and numerous. However, in black grouse scat, the total seed load and the *V. myrtillus* seed load and seedling detection probability was lower compared to the omnivores. Seedlings of *V. vitis-idaea* were almost as probable to detect as *V. myrtillus*, and *V. uliginosum* was found emerging from only one scat. Berries of *Vaccinium* species are known to be eaten by black grouse (Kashevarov & Pozdnyakov, 1997; Welch et al., 2000) and capercaillie (Summers et al., 2004; Borchtchevski, 2009), and seedlings of *V. myrtillus* has emerged from capercaillie and red grouse (*Lagopus lagopus scotius*) scat in a previous study (Welch et al., 2000), so these findings are not surprising. *Vaccinium vitis-idaea* comprised a larger proportion of the germinating seeds in scats from tetraonids compared to scats from omnivores (Fig. 3). Also, tetraonid-mediated *V. myrtillus* dispersal decreased in autumn, while the omnivores continued to commonly disperse *V. myrtillus* in autumn (Fig. 5). It seemed that the tetraonids were relatively more important dispersers for *V. vitis-idaea* than *V. myrtillus* compared to the omnivores.

Graminoid seedlings were often found emerging from scats of both capercaillie and black grouse, and the seed load of graminoids in capercaillie scat was significantly higher compared to scats from omnivores. While omnivores feed on graminoid leaves (Persson et al., 2001; D'hondt et al., 2011), rush seeds are part of the black grouse's diet (Starling, 1992; Starling-Westerberg, 2001; Beeston et al., 2005), and seeds from sedges and grasses are included in the capercaillie's diet (Moss & Picozzi, 1994; Kashevarov & Pozdnyakov, 1997; Summers et al., 2004). Since being granivores, tetraonids should therefore ingest more graminoid seeds compared to the omnivores, but since the tetraonids disintegrate the seeds for their nutrition, relatively few seeds should remain viable after passing the tetraonid digestive tract (Welch et al., 2000; Orłowski & Czarnecka, 2013). Seeds from *Juncus* spp. and other herbs have earlier been found in black grouse scats (Starling, 1992), and in scats from other tetraonids, the grey partridge (*Perdix perdix*) (Orłowski & Czarnecka, 2013, Orłowski et al., 2016) and the red grouse (Welch, 1985). It is possible that the effect of ingesting many seeds at once may outweigh the negative effects of a destructive digestion system, like in tetraonids (Orłowski & Czarnecka, 2013), or cattle (*Bos taurus*) (Bruun & Poschlod, 2006). Even if only few of the ingested seeds survive the gut passage of tetraonids (Welch et al., 2000), a few surviving seeds can be important for the dispersal and sexual regeneration of a plant species (Cain et al., 2000; Gillespie et al., 2012; Orłowski et al., 2016). In this study, the capercaillie was the only species dispersing more than three viable graminoid seeds per scat, but other animals have also proven to be effective graminoid dispersers, for example roe deer and red deer (Jaroszewicz et al., 2013; Picard et al., 2016), and greylag goose (*Anser anser*) (Hattermann et al., in press)

The low number of seedlings found emerging from scats from herbivores suggest that the herbivores are not important as endozoochorical seed disperses in the boreal forest. Both moose and mountain hare dispersed much fewer viable seeds compared to the omnivores and tetraonids. The fact that only a few seedlings emerged from a relatively large amount of moose scat was surprising, as the moose dispersed viable seeds from several plant species (including graminoids and forbs) in the mixed deciduous forest of Białowieża in Poland (Jaroszewicz et al., 2013). The probability of detecting seedlings emerging from moose scats in Białowieża was 51% (Jaroszewicz et al., 2013), compared to only 3% in summer and no findings in autumn in this study. However, the seed load in moose scat in Białowieża was also relatively low (Jaroszewicz et al., 2013). Since graminoids and forbs are included in the moose diet (Wam & Hjeljord et al., 2010; Jaroszewicz et al., 2013), I expected to find such seedlings. During summer, however, the moose feeds mainly on leaves from bushes and trees (e.g. rowan, birch

and willow) (Wam & Hjeljord et al., 2010), which may lead to a low seed intake (Jaroszewicz et al., 2013; Picard et al., 2016).

Few faecal pellet groups from mountain hare were found. The hare dispersed a low seed load (0.3 seedlings/g dry scat), which resembled what has been found for European hare (*Lepus europaeus*) and rabbit (*Oryctolagus cuniculus*), where the seed load has ranged from 0.2 to 6.5 seedlings per gram dry scat (Malo & Suárez, 1995; Heinken et al., 2002; Pakeman et al., 2002; Eycott et al., 2007). The broad summer diet of the mountain hare consists of leaves and twigs from bushes and herbs (Pulliainen, 1972; Angerbjörn, 1995), and suggests that the hare unintentionally can ingest seeds from many plant species. However, I only detected two species emerging from their faeces. Since the seed load was similar compared to other studies, the reason for few species detected could be that few hare scats were found. No seedlings emerged from beaver scats, even though they feed on forbs and graminoids during summer (Svendsen, 1980; Krojerová-Prokesová et al., 2010), and seeds have been found in their scats (Krojerová-Prokesová et al., 2010). The low number of samples and the fact that beavers usually consume stems and roots rather than flowers and fruits (Simonsen, 1973; Svendsen, 1980; Haarberg & Rosell, 2006), probably explains the absence of seedlings emerging from their scats in this study. All three herbivores have long, complex and seed-destructive digestion systems including repeated chewing and coprophagy for hare and beaver (Hörnicke & Björnhag, 1980; Angerbjörn, 1995; Eycott et al., 2007; Fedriani & Delibes, 2009; Krojerová-Prokesová et al., 2010; Jaroszewicz et al., 2013; Picard et al., 2016). The complex digestion system combined with a possibly lower seed intake compared to omnivores and tetraonids, probably explains the lower seed load and lower probability of germinating seeds in scats from herbivore compared to scats from omnivores and tetraonids.

The probability of detecting germinating seeds in scats and the seed load for some plant species in scats was better explained by the season compared to the disperser species. The amounts of *V. vitis-idaea* and *V. uliginosum* increased from summer to autumn, while the seed load of *V. myrtillus* remained stable, which can be explained by plant phenology. The two former mentioned plants set fruit later than *V. myrtillus* (Eriksson & Ehrlén, 1991; Fitter & Peat, 1994), and the berry diet of the animals often reflects which fruits are available at a given time (Herrera, 1989; Starling-Westerberg, 2001; Schaumann & Heinken, 2002; D'hondt et al., 2011; Stenset et al., 2016). The brown bear is known to eat overwintered *V. myrtillus* berries in spring (Elgmork & Kaasa, 1992; Stenset et al., 2016), which can explain the similar detection probabilities for *V. myrtillus* for summer and autumn in bear scat. The summer of 2018 was

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warmer than normal summers (Grinde et al., 2018; Jonsson, 2018), and increased temperatures have shown to hasten the ripening of berries (Eriksson & Ehrlén, 1991; Wipf et al., 2009), which was observed during fieldwork in July (they were ripe before mid-July, the normal start of the berry season (Stenset et al., 2016)), and could explain the relatively high detection probabilities of *V. myrtillus* emerging from summer scats. During summers with more normal temperatures, I would probably have observed a larger difference between the two seasons, as a larger portion of the *Vaccinium* seedlings probably would have been detected emerging from the autumn scats.

Characteristics and differences of the seed dispersal niches

Regarding the probability of detecting seedlings and the dispersed seed load (for all and for specific plant taxa), it appeared that the variation was larger between the three groups of dispersers (omnivores, tetraonids and herbivores) than within those groups. This indicates seed dispersal niche variation between those three groups, probably explained by behavioural and/or physiological differences between the animals. In addition to the differences regarding *V. myrtillus* and graminoids discussed in the previous sections, the omnivores dispersed a higher and more variable seed load than the tetraonids. Seeds of dry-fruited species are a part of the tetraonid diet (e.g. Starling, 1992; Summers et al., 2004), which implies that they should destroy a large portion of the seeds when digesting (Welch et al., 2000; Orłowski & Czarnecka, 2009). This contrasts with the omnivores who use the fruit pulp, not the seeds, as the nutritional component, and they should therefore destroy few seeds since the seed intake mostly is a consequence of their berry diet (Herrera, 1989; Koike et al., 2008; Tsuji et al., 2011). The reason for the higher seed load dispersed by omnivores could also be because of higher seed intake (Bruun & Poschlod, 2006), as especially the brown bear and the red fox can consume large numbers of berries (D'hondt et al., 2011; Stenset et al., 2016), while berries just are a part of the broad tetraonid diet (Starling-Westerberg, 2001; Summers et al., 2004; Beeston et al., 2005; Borchtchevski, 2009) and a *V. myrtillus* berry can contain more than 70 seeds (Ranwala & Naylor, 2004). The high variance in the seed load dispersed by omnivores could be because they feed on both plant and animal matter. The omnivores can act as true carnivores, which may cause scats consisting entirely of animal remains, thus dispersing a low seed load, or as pure frugivores, resulting in high seed loads in scats (Herrera, 1989).

Despite the differences between the seed dispersal niches of the different dispersers, their niches did to a large degree contain the same plant species. The nestedness temperature of the seed

dispersal niches was 1.34, which is low according to Rodríguez-Gironés & Santamaría, (2006), and indicates that the seed dispersal niches in this study form close to a perfectly nested system. Thus, the plant species detected in the less species-rich seed dispersal niches (of e.g. the pine marten) are also detected in the more species-rich seed dispersal niches (of e.g. the red fox). Some plant species was detected in scats from only one disperser species, but there were no signs of plants adapted especially to one disperser, as these plant species only were found emerging from one scat each. Even though the red fox dispersed the largest number of plant taxa, the seed dispersal niche of the capercaillie was the most diverse, probably because the niche was more evenly shared among several plant taxa. Despite relatively many species, the seed dispersal niche of the brown bear got a lower diversity score compared to for example pine marten and black grouse, probably because the proportion of viable *V. myrtillus* seeds was larger in brown bear scats.

The habitat and traits of the dispersed plant species have not been thoroughly studied in this study, mainly because of a low number of plant species detected. However, in this study, most seedlings comprised characteristic field layer species of the boreal forest in the study area (Swenson et al., 1999), and most produce fleshy fruits. More species with dry fruits than species with fleshy fruits were detected, but a larger portion of the fleshy-fruited than the dry-fruited species in the Scandinavian boreal forests were dispersed (Lid et al., 2005). Only one large (>1 mg (Fitter & Peat, 1994; Heinken et al., 2002)) seed *(Malus domestica)* germinated, supporting findings saying that small seeds get dispersed more often by endozoochory compared to large seeds (Heinken et al., 2002; Pakeman et al., 2002; Albert et al., 2015; Picard et al., 2016). This study gives little support to the "Foliage is the fruit hypothesis" in the boreal forest ecosystem, as the terrestrial mammalian herbivores in this study (moose and hare) (Janzen, 1984; Willson, 1993) dispersed very few viable seeds.

Effective and important seed dispersers
A high seed load compared to other animal groups, as found in scats from omnivores in this study, and enhanced germination in scats found in earlier studies on endozoochory by omnivores (Traveset et al., 2001; Schaumann & Heinken, 2002), are traits of effective seed dispersers (Schupp et al., 2010). However, when considering an entire ecosystem, other animal groups (e.g. tetraonids) can be equally important seed dispersers due to a larger local abundance (Schupp et al., 2010). Considering the seed loads found in this study, the populations of brown bear, red fox, pine marten, capercaillie and black grouse are together able to disperse huge

quantities of seeds (Table 3), and probably over large distances. The dispersal distances with brown bear as the disperser can easily reach 1.5 kilometres (Lalleroni et al., 2017), and seeds are often dispersed farther (Steyaert et al., Unpublished). The red fox, marten and capercaillie can also transport seeds more than 1 kilometre (Otani, 2002; Jordano et al., 2007; Rost et al., 2012; Evstigneev et al., 2017). The area in which the black grouse disperses seeds is likely their home ranges, which are about 0.5 square kilometres for cocks (Eggestad et al., 1988; Rolstad et al., 1988). However, all these species can disperse seeds farther in migration, which could lead to longer seed dispersal distances (Nathan et al., 2008). That seeds get dispersed more than 1 kilometre from the parent population is often termed "long-distance dispersal" (Nathan et al., 2008). This can be beneficial for plant populations in terms of genetic exchange and colonization, and the migration rate to areas with suitable habitats can be much higher compared to migration rates by unassisted dispersal of seeds (Clark et al., 1998; Cain et al., 2000, Nathan et al., 2008).

The dispersal of seeds by animals can be more successful for the plant if the seeds are subjects to "directed dispersal" (i.e. disproportionate seed dispersal to ideal germination and establishment conditions) compared to seed dispersal to a random location (Howe & Smallwood et al., 1982; Schupp et al., 2010). *Vaccinium* species, and *V. myrtillus* in particular, germinate and establish almost exclusively in disturbed patches like rotting logs and exposed soil, and very rarely in a vegetated ground layer (Eriksson & Fröborg, 1996). *Vaccinium* seedlings are rarely found in patches where adult *Vaccinium* already dominate (Eriksson & Fröborg, 1996; Welch et al., 2000), so dispersers are needed to transport seeds to unoccupied patches with favourable establishment conditions. Frugivorous carnivores have been shown to do this (Jordano et al., 2007). The marten can defecate on stumps and logs (Pulliainen, 1982; Schaumann & Heinken, 2002), the brown bear in its resting sites (Steyaert et al., 2012) and the red fox in disturbed vegetation at carcass sites (Steyaert et al., 2018) and in burnt forests (Rost et al., 2012). Endozoochorical seed dispersal can contribute to faster regrowth and a greater diversity of vegetation on disturbed patches and degraded habitats (Howe & Miriti, 2004). For some plant species adapted to endozoochory, vertebrate seed dispersal vectors are needed to maintain the populations and distribution of the plant species (Ozinga et al., 2009; Markl et al., 2012)

The amount of seeds dispersed in an area and the potential for directed dispersal, suggests that the studied animals can redistribute seeds and disperse plant species to new locations. In a rapidly changing world, seed dispersal by animals can be important for maintaining biodiversity

in ecosystems, and vital for the survival of some plant species (Cain et al., 2000; Ozinga et al., 2009; Jordano et al., 2011). An example is the cloudberry (*Rubus chamaemorus*), which did not appear in this study, but is thought to be dispersed by birds and omnivores (Taylor, 1971; Rantala, 1976), and which seeds were found in red fox scats (Steyaert, 2019). The distribution of *R. chamaemorus* is predicted to decrease due to climate changes, and in Europe it may survive only in Scandinavia (Harrison et al., 2006). *Rubus chamaemorus*, and probably many other plant species will need their long-distance dispersal vectors to track their preferred climatic conditions (Harrison et al., 2006; McConkey et al., 2012). This highlights the necessity of sufficient size and distribution of seed dispersers, as they probably are needed to regenerate plant populations and redistribute plant species after disturbances and during climate change (Ozinga et al., 2009).

Sources of error and the ecological significance of this study

This study may not give a completely accurate picture of the endozoochorical seed dispersal in the boreal forest. Seeds from all plant species present in the scats may not have been able to germinate under the conditions they were exposed to. For example, crowberry needs prolonged frost stratification to germinate (Bell & Tallis, 1973), so it was probably under-represented in the results. Also, some seedlings (e.g. raspberry *Rubus idaeus*) emerged after I had stopped counting seedlings for the master thesis. In addition, several potential seed dispersers were not included in this study, among them roe deer, red deer, wild boar, gray wolf, and most rodents and birds, which implies that some plant groups may be under-represented. While omnivores more often defecate on tracks and roads than in the surrounding area, the ruminants avoid these structures when defecating (Suárez-Esteban et al., 2013). This could be the reason for the absence of roe deer scat in this study.

To get more precise assessments of the endozoochorical seed dispersal niches in the boreal forest, there are improvements that can be done in later studies on the topic. Firstly, vegetation surveys to assess plant availability can be performed. Secondly, scat sampling can include opportunistic sampling in addition to sampling on tracks, to increase the number of scats from cervids. Thirdly, the diet of the dispersers could be assessed by DNA barcoding of the scat to relate the ingested plant species to the plant species germinating from scats. Fourthly, the germination trial should continue until all seeds have germinated and include a frost stratification. If the goal of a study is to determine the species of all plants germinating from scats, DNA barcoding of seedlings should be applied. Further, similar studies can be done in

boreal forests elsewhere in Scandinavia to include more plant species and compare seed dispersal in different plant and disperser communities.

Dispersal by animals also includes epizoochory, and synzoochory (Howe & Smallwood, 1982; Nathan et al., 2008; Gillespie et al., 2012). Consequently, this study only encompasses an unknown part of the total zoochorous seed dispersal in the boreal forest. It has been shown that results of endozoochory studies tend to over-estimate the seed dispersal potential of the animals studied when the germination trial is conducted in controlled climatic conditions (Pakeman & Small, 2009). The results of this study represent which seeds that potentially can be dispersed by endozoochory, as most of these seeds would probably never have become adult plants if left in nature, due to for example pathogens, competition, or the lack of a suitable habitat (Howe & Miriti, 2004; Pakeman & Small, 2009). However, for the studied animal species, these results provide a solid base for further studies on the roles and effectiveness of the endozoochorous seed dispersers in the boreal forest.

Conclusions

This study highlights the large potential of medium-sized and large birds and mammals to disperse seeds of plants in the boreal forest of southcentral Sweden. Scats from several of the studied animal species often contained germinating seeds, and the animals often dispersed viable seeds in large quantities. Both omnivores and tetraonids dispersed considerable amounts of viable seeds, while the herbivores seemed not to do so. The omnivores dispersed more viable seeds per gram dry scat compared to the tetraonids, but the number of plant species dispersed were similar. Most emerging seedlings belonged to the fleshy-fruited forest floor species of the *Vaccinium* genus, indicating that a fleshy fruit is a good adaptation to dispersal by some of the studied dispersers. Since seedlings of dry-fruited species were found rarer and in lower numbers compared to fleshy-fruited species, plant species with dry fruits in this area seem to be less adapted to endozoochory by the studied dispersers compared to fleshy-fruited species. The dispersal niches of the different animal species resembled each other, due to the dominance of *Vaccinium* spp. emerging from scats. The plant species that germinated coincided to a large degree with the diet of the animals, and the omnivores dispersed more viable seeds per gram dry scat than the other animal groups, indicating that diet and digestion are important factors determining the species and quantity of plants dispersed.

Several of the species in this study (e.g. moose, capercaillie, *V. myrtillus* and *V. vitis-idaea*) are species commonly harvested in Scandinavia, and are therefore of interest for the public and for managers. Animals have an important role as providers for ecosystem services, as exemplified with endozoochorical seed dispersal in this study. Studies like this can increase the knowledge about ecosystem services provided by animals and thus increase awareness of consequences of wildlife management regimes.

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Appendix

	Brown bear (n=13)	Red fox (n=63)	Pine marten (n=55)	Moose (n=37)	Mountain hare (n=8)	Capercaillie (n=60)	Black grouse (n=59)
Betula pubescens		1					
Calluna vulgaris		2					
Carex spp.		1				4	
Empetrum nigrum	1	1					
Fragaria vesca		3					
Gnaphalium uliginosum							1
Juncus articulatus		1					
Juncus bufonius						2	2
Juncus sp.						1	2
Malus domestica	1						
Omalotheca sylvatica						1	
Oxycoccus spp.	1	5	1			1	
Poaceae spp.	1	4				5	3
Plantago major	1					1	
Sagina sp.		1					
Senecio vulgaris			1				
Vaccinium myrtillus	11	40	23	1	1	9	16
Vaccinium uliginosum	5	13	3			7	1
Vaccinium vitis-idaea	4	15	12		2	17	19
Unid. dry-fruited ericoid	2	1					
Unidentified graminoids		2					
Total n taxa	9	13	5	1	2	10	7

Appendix 2. *Estimated difference (with Tukey pairwise comparison test) between disperser species regarding seedling probability in scats of all plant species, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a binomial fitted GLM with seedling probability as response and disperser species as explanatory variable. UA=brown bear, VV=red fox, MM=pine marten, LT=mountain hare, AA=moose, TU=capercaillie and TT=black grouse. *, **, and *** indicate increasingly stronger significant differences.*

Species	Estimate	Std. Error	z value	Pr(>|z|)
LT vs. AA	3.07269	1.24944	2.459	0.15012
MM vs. AA	3.62126	1.05036	3.448	0.00870 **
TT vs. AA	4.03154	1.04834	3.846	0.00208 **
TU vs. AA	3.65021	1.04619	3.489	0.00712 **
UA vs. AA	5.45532	1.26676	4.307	< 0.001 ***
VV vs. AA	4.88977	1.06091	4.609	< 0.001 ***
MM vs. LT	0.54857	0.78028	0.703	0.99080
TT vs. LT	0.95885	0.77755	1.233	0.86253
TU vs. LT	0.57752	0.77464	0.746	0.98747
UA vs. LT	2.38263	1.05369	2.261	0.23137
VV vs. LT	1.81708	0.79441	2.287	0.21917
TT vs. MM	0.41028	0.38309	1.071	0.92529
TU vs. MM	0.02895	0.37715	0.077	1.00000
UA vs. MM	1.83406	0.80773	2.271	0.22714
VV vs. MM	1.26851	0.41624	3.048	0.03044 *
TU vs. TT	-0.38133	0.37148	-1.027	0.93855
UA vs. TT	1.42378	0.80510	1.768	0.53023
VV vs. TT	0.85823	0.41111	2.088	0.32328
UA vs. TU	1.80511	0.80229	2.250	0.23691
VV vs. TU	1.23956	0.40558	3.056	0.02988 *
VV vs. UA	-0.56555	0.82139	-0.689	0.99179

Appendix 3. *Estimated difference (with Tukey pairwise comparison test) between disperser species regarding seed load of all plant species, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a gamma fitted GLM with seed load as response and disperser species as explanatory variable. UA=brown bear, VV=red fox, MM=pine marten, LT=mountain hare, AA=moose, TU=capercaillie and TT=black grouse. *, **, and *** indicate increasingly stronger significant differences.*

Species	Estimate	Std. Error	z value	Pr(>|z|)
AA vs. VV	-5.8691	1.3658	-4.297	< 0.001 ***
LT vs. VV	-3.1032	0.8045	-3.858	0.00159 **
MM vs. VV	-0.3521	0.3252	-1.083	0.91929
TT vs. VV	-1.4393	0.2980	-4.829	< 0.001 ***
TU vs. VV	-1.0216	0.3115	-3.280	0.01392 *
UA vs. VV	-0.7599	0.4226	-1.798	0.50276
LT vs. AA	2.7659	1.5609	1.772	0.52084
MM vs. AA	5.5170	1.3766	4.008	< 0.001 ***
TT vs. AA	4.4298	1.3704	3.233	0.01630 *
TU vs. AA	4.8475	1.3734	3.530	0.00591 **
UA vs. AA	5.1092	1.4028	3.642	0.00398 **
MM vs. LT	2.7511	0.8226	3.344	0.01128 *
TT vs. LT	1.6639	0.8123	2.048	0.33930
TU vs. LT	2.0816	0.8173	2.547	0.11844
UA vs. LT	2.3433	0.8658	2.706	0.07858
TT vs. MM	-1.0871	0.3441	-3.159	0.02086 *
TU vs. MM	-0.6695	0.3558	-1.881	0.44584
UA vs. MM	-0.4078	0.4563	-0.894	0.96737
TU vs. TT	0.4176	0.3312	1.261	0.84570
UA vs. TT	0.6794	0.4374	1.553	0.67246
UA vs. TU	0.2617	0.4467	0.586	0.99646

Appendix 4. *Estimated difference (with Tukey pairwise comparison test) between disperser species and between seasons regarding seedling probability of Vaccinium myrtillus in scats, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a binomial fitted GLM with seedling probability as response and disperser species and season as additive explanatory variables. UA=brown bear, VV=red fox, MM=pine marten, LT=mountain hare, AA=moose, TU=capercaillie and TT=black grouse. Under "Season" heading, 1=May-July and 2=July-September. *, **, and *** indicate increasingly stronger significant differences.*

Species	Estimate	Std. Error	z value	Pr(>|z|)
AA vs. VV	-2.5350	1.5061	-1.683	0.59383
LT vs. VV	-3.2281	1.3297	-2.428	0.16399
MM vs. VV	0.2558	0.6815	0.375	0.99973
TT vs. VV	-2.1650	0.5577	-3.882	0.00162 **
TU vs. VV	-2.7079	0.5928	-4.568	< 0.001 ***
UA vs. VV	-0.2902	0.7816	-0.371	0.99975
LT vs. AA	-0.6931	1.8708	-0.371	0.99975
MM vs. AA	2.7908	1.5609	1.788	0.52108
TT vs. AA	0.3700	1.4680	0.252	0.99997
TU vs. AA	-0.1729	1.4866	-0.116	1.00000
UA vs. AA	2.2448	1.6009	1.402	0.77670
MM vs. LT	3.4840	1.3915	2.504	0.13718
TT vs. LT	1.0632	1.2865	0.826	0.97902
TU vs. LT	0.5202	1.3077	0.398	0.99963
UA vs. LT	2.9380	1.4363	2.046	0.35174
TT vs. MM	-2.4208	0.6846	-3.536	0.00624 **
TU vs. MM	-2.9637	0.7125	-4.160	< 0.001 ***
UA vs. MM	-0.5460	0.8709	-0.627	0.99515
TU vs. TT	-0.5429	0.5479	-0.991	0.94875
UA vs. TT	1.8748	0.7781	2.409	0.17102
UA vs. TU	2.4177	0.8036	3.009	0.03550 *
Season				
2 vs. 1	-1.4125	0.4345	-3.251	0.00115 **

Appendix 5. *Estimated difference (with Tukey pairwise comparison test) between disperser species and between seasons regarding seed load of Vaccinium myrtillus, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a gamma fitted GLM with seed load as response and disperser species and season as additive explanatory variables. UA=brown bear, VV=red fox, MM=pine marten, LT=mountain hare, AA=moose, TU=capercaillie and TT=black grouse. Under "Season" heading, 1=May-July and 2=July-September. *, **, and *** indicate increasingly stronger significant differences.*

Species	Estimate	Std. Error	z value	Pr(>|z|)
AA vs. VV	-5.53127	1.25071	-4.423	< 0.001 ***
LT vs. VV	-1.88202	1.25071	-1.505	0.70299
MM vs. VV	0.05328	0.32207	0.165	1.00000
TT vs. VV	-1.14055	0.37026	-3.080	0.02655 *
TU vs. VV	-1.24420	0.46575	-2.671	0.08579
UA vs. VV	-0.47657	0.41808	-1.140	0.89805
LT vs. AA	3.64925	1.73652	2.101	0.30724
MM vs. AA	5.58455	1.26436	4.417	< 0.001 ***
TT vs. AA	4.39072	1.26738	3.464	0.00737 **
TU vs. AA	4.28706	1.29465	3.311	0.01251 *
UA vs. AA	5.05469	1.29040	3.917	0.00133 **
MM vs. LT	1.93530	1.26436	1.531	0.68593
TT vs. LT	0.74147	1.26738	0.585	0.99646
TU vs. LT	0.63782	1.29465	0.493	0.99864
UA vs. LT	1.40545	1.29040	1.089	0.91653
TT vs. MM	-1.19383	0.41058	-2.908	0.04459 *
TU vs. MM	-1.29749	0.50000	-2.595	0.10437
UA vs. MM	-0.52985	0.45044	-1.176	0.88338
TU vs. TT	-0.10366	0.51291	-0.202	0.99999
UA vs. TT	0.66397	0.48710	1.363	0.79021
UA vs. TU	0.76763	0.56346	1.362	0.79070
Season				
2 vs. 1	-0.2997	0.2614	-1.147	0.252

Appendix 6. *Estimated difference (with Tukey pairwise comparison test) between disperser species when interacting with season regarding seedling probability of Vaccinium uliginosum in scats, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a binomial fitted GLM with seedling probability as response and disperser species and season as interacting explanatory variables. UA=brown bear, VV=red fox, MM=pine marten, TU=capercaillie and TT=black grouse. Under "Season" heading, 1=May-July and 2=July-September. *, **, and *** indicate increasingly stronger significant differences.*

Species	Estimate	Std. Error	z value	Pr(>|z|)
Season 1				
UA vs. TU	0.7985	1.1255	0.709	0.478
Season 2				
MM vs. VV	-1.5404	0.7474	-2.061	0.2274
TT vs. VV	-2.7081	1.1048	-2.451	0.0964
TU vs. VV	-1.2528	0.6894	-1.817	0.3513
UA vs. VV	-0.5108	0.8290	-0.616	0.9710
TT vs. MM	-1.1676	1.2130	-0.963	0.8659
TU vs. MM	0.2877	0.8522	0.338	0.9970
UA vs. MM	1.0296	0.9686	1.063	0.8178
TU vs. TT	1.4553	1.1782	1.235	0.7204
UA vs. TT	2.1972	1.2649	1.737	0.3983
UA vs. TU	0.7419	0.9245	0.802	0.9263

Appendix 7. *Estimated difference (with Tukey pairwise comparison test) between seasons regarding seed load of Vaccinium uliginosum, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a gamma fitted GLM with seed load as response and season as explanatory variable. 1=May-July and 2=July-September. *, **, and *** indicate increasingly stronger significant differences.*

Season	Estimate	Std. Error	z value	Pr(>|z|)
2 vs. 1	2.973	0.786	3.783	0.000155 ***

Appendix 8. *Estimated difference (with Tukey pairwise comparison test) between disperser species and between seasons regarding seedling probability of Vaccinium vitis-idaea, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a binomial fitted GLM with seedling probability as response and disperser species and season as additive explanatory variables. UA=brown bear, VV=red fox, MM=pine marten, LT=mountain hare, AA=moose, TU=capercaillie and TT=black grouse. Under "Season" heading, 1=May-July and 2=July-September. *, **, and *** indicate increasingly stronger significant differences.*

Species	Estimate	Std. Error	z value	Pr(>|z|)
AA vs. VV	-12.6319	882.7435	-0.014	1.000
LT vs. VV	2.6273	1.3009	2.020	0.338
MM vs. VV	0.4963	0.5378	0.923	0.958
TT vs. VV	1.2769	0.5140	2.484	0.128
TU vs. VV	1.0962	0.5239	2.092	0.296
UA vs. VV	-0.1568	0.7218	-0.217	1.000
LT vs. AA	15.2592	882.7442	0.017	1.000
MM vs. AA	13.1283	882.7435	0.015	1.000
TT vs. AA	13.9089	882.7435	0.016	1.000
TU vs. AA	13.7281	882.7435	0.016	1.000
UA vs. AA	12.4751	882.7437	0.014	1.000
MM vs. LT	-2.1310	1.3254	-1.608	0.616
TT vs. LT	-1.3504	1.2878	-1.049	0.924
TU vs. LT	-1.5311	1.3065	-1.172	0.876
UA vs. LT	-2.7841	1.4160	-1.966	0.371
TT vs. MM	0.7806	0.5733	1.362	0.778
TU vs. MM	0.5998	0.5822	1.030	0.929
UA vs. MM	-0.6531	0.7653	-0.853	0.971
TU vs. TT	-0.1808	0.5457	-0.331	1.000
UA vs. TT	-1.4337	0.7537	-1.902	0.412
UA vs. TU	-1.2530	0.7579	-1.653	0.584
Season				
2 vs. 1	1.8142	0.3892	4.662	3.14e-06 ***

Appendix 9. *Estimated difference (with Tukey pairwise comparison test) between seasons regarding seed load of Vaccinium vitis-idaea, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a gamma fitted GLM with seed load as response and season as explanatory variable. 1=May-July and 2=July-September. *, **, and *** indicate increasingly stronger significant differences.*

Season	Estimate	Std. Error	z value	Pr(>|z|)
2 vs. 1	1.3604	0.3658	3.719	2e-04 ***

Appendix 10. Estimated difference (with Tukey pairwise comparison test) between disperser species regarding seed load of graminoids, and the corresponding standard error, z-, and p value. Seedlings derive from scats collected in the boreal forest of southcentral Sweden summer and autumn 2018. The Tukey test was based on a gamma fitted GLM with seed load as response and disperser species as explanatory variable. UA=brown bear, VV=red fox, MM=pine marten, LT=mountain hare, EA=moose, TU=capercaillie and TT=black grouse. *, **, and *** indicate increasingly stronger significant differences.

Species	Estimate	Std. Error	z value	Pr(>|z|)
TT vs. VV	1.8511	0.8474	2.184	0.1173
TU vs. VV	3.5158	0.7364	4.774	<0.001 ***
UA vs. VV	-0.7569	1.6283	-0.465	0.9644
TU vs. TT	1.6647	0.7730	2.154	0.1259
UA vs. TT	-2.6080	1.6452	-1.585	0.3687
UA vs. TU	-4.2728	1.5909	-2.686	0.0332 *