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Factors affecting the distribution of the invasive American mink *Neovison vison* in a riparian landscape in Central Norway.

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Preface

This master's thesis is written as part of the project "Sjøørret i Steinkjer" (Sea trout in Steinkjer). The thesis concludes my master's degree in biosciences with specialization in terrestrial ecology and nature management at the Faculty of Biosciences and Aquaculture, Nord University.

It has been challenging work, and many hours have been put into the project. I owe my gratitude to those who have helped me with the fieldwork. Bror Mathias Bonde, Lasse Bruun, Kristine Berentsen, Martin Eldøy, Mie Prik Arnberg, Therese Mikalsen, and especially Andreas Baskår Pedersen; I truly appreciate their help.

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Thanks to my wonderful wife for being who you are and supporting me all the time. Soon our new adventure begins.

Finally, I want to thank my supervisor Sam Steyaert for assistance with the study design, fieldwork, statistics, and all the excellent feedback and tips on the writing of this thesis. It has been a privilege having you as my supervisor. Thank you.

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Abstract

Invasive mammalian predators, such as the American mink (*Neovison vison*), are highly adaptable, spread fast, and represent a hazard to native species through habitat occupancy, competition, and predation. Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) make up for a large portion of the minks' diet in rivers throughout Scandinavia. The anadromous trout, the sea trout, is currently at a historically low level in Central Norway. Conventional ecological theory predicts that apex predators, such as the Eurasian otter can displace or outcompete mesopredators such as mink, and thus indirectly benefit the minks' prey species.

This study aims to investigate if competitors and especially otter, affect the spatial distribution of mink in a riparian landscape in addition to the effects of environmental factors such as vegetation types and water velocity.

By using logistic regression, the occurrence of feral mink across the study system was modelled in relation to sympatric vertebrate species (including potential prey, predators, and competitors), the relative density of their main prey (salmon and trout), and habitat characteristics (both aquatic and terrestrial).

The results show that the presence of passerines and spruce positively affects the detection rate of mink, while bank height has a negative effect. With increasing bank height, the detection rate of mink decreases. None of the competitors seem to affect mink detection. Mink seems to prefer areas with higher densities of trout.

Otters probably have a minimal effect on mink distribution in the watercourse due to the riparian landscape homogeneous nature, good access to terrestrial prey, and that mink have the possibility to segregate from the larger otter. Trapping campaigns for mink should consider the variables pointing to the preferred areas to be more successful in the adaptive management of mink.

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1. Introduction

Invasive mammalian predators are perhaps the most damaging group of alien animal species for global native biodiversity (Bellard, Genovesi, & Jeschke, 2016; Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). Invasive mammalian predators are often generalists with a high reproduction rate, adapt easily to new environments, and tend to spread fast (Caut, Angulo, & Courchamp, 2008; Macdonald & Harrington, 2003). Invasive predators may outperform native species through habitat occupancy, competition, and predation (Doherty et al., 2016). Suppression of native species could lead to their decline and even extinction, and can cascade throughout the entire ecosystem (Banks et al., 2008; Bellard et al., 2016; David et al., 2017). Understanding and mitigating the impact of invasive mammalian predators is essential for reducing the rate of biodiversity loss (Doherty et al., 2016).

The American mink (hereafter mink; *Neovison vison*) was introduced to Scandinavia in the 1920s for commercial fur farming (Bevanger & Henriksen, 1995). Already at the time, researchers warned for introducing an alien predator into Norway, as it could invade native ecosystems (Lysvold & Kalkenberg, 2016). In Norway, only small colonies of feral mink occurred around the mink farms until the 1950s, but through continuous escapes and deliberate releases, the mink successfully colonized the entire country within a few decades, except for some coastal islands (Bevanger & Henriksen, 1995; Pedersen, Swenson, & Syvertsen, 2018). The mink is a semi-aquatic mammal that thrives best in coastal areas. Nevertheless, they are also frequently observed inland and even up in mountainous terrain, usually connected to waterways (Pedersen et al., 2018). Being semi-aquatic, the mink catches prey both on land and in the water (Bonesi, Chanin, & Macdonald, 2004). Like all mustelids, they store food and are capable to do great harm in ground-nesting sea-bird colonies and to other ground nesters, but also in mammals such as water voles (*Arvicola amphibius*) and other small rodents (*Rodentia* sp.) (Banks et al., 2008; Carter & Bright, 2003; Craik, 1997; Dunstone & Birks, 1987). The diet of the mink varies with the seasons, and according to prey availability, topography, and hydromorphology (Chanin & Linn, 1980). In freshwater systems, fish, especially small anadromous salmonids like brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) are at risk of predation. Previous studies have shown that fish is an important part of mink diet (20 – 60 %), and local mink induced fish mortality rates as high as 80 % have been reported (Heggenes & Borgstrøm, 1988; Kauhala, 1996; Wolff, Taylor, Heske, & Schooley, 2015). The mink is considered as a destructive invasive species across Europe because of its high invasion

potential and strong negative effects on biodiversity, including negative impacts on several IUCN red listed and vulnerable species (Ahlers, Heske, & Schooley, 2016; Gederaas, Moen, Skjelseth, & Larsen, 2012). The corncrake (*Crex crex*) which is rated as critically endangered (CR) in Norway and the common eider (*Somateria mollissima*) (near threatened, NT) are both examples of vulnerable ground nesting birds that suffer from mink predation (Heggøy & Øien, 2016; Stien & Ims, 2016). The mink has few natural enemies in Norway, and besides some carnivores, humans are their main threat (Schlimme, 2003). Mink is also known to be aggressive and will defend themselves from animals much larger than themselves (Schlimme, 2003).

Apex predators play a vital role in maintaining healthy and balanced ecosystems (Elmhagen, Ludwig, Rushton, Helle, & Lindén, 2010; Estes et al., 2011). Mesopredator suppression theory predicts that apex predators can displace or outcompete mesopredators, and thus indirectly benefit mesopredator prey species (Gordon, Feit, Grüber, & Letnic, 2015). Such trophic cascades can have profound impacts on local community compositions (Elmhagen et al., 2010; Pace, Cole, Carpenter, & Kitchell, 1999). In many ecosystems around the world, apex predators have disappeared, leading to mesopredators to thrive. This mechanism is also referred to as the Mesopredator Release Hypothesis (MRH) (Soulé et al., 1988). The Scandinavian indigenous Eurasian otter (hereafter otter; *Lutra lutra*) was one of the main apex predators in coastal areas and inland rivers and lakes up until the 1950s (Hagström, Hagström, & Lundwall, 2011). Between the 1950s and 1980s the Scandinavian otter population drastically declined, mostly due to anthropogenic factors like hunting and environmental toxic chemicals like polychlorinated biphenyl (PCB) and dichlorodiphenyltrichloroethane (DDT) which affected their fertility (Heggberget, 1988; Tison et al., 2015). Today, otters are found all over the country, but mainly in coastal regions from central and northern Norway. Otters are also occasionally observed inland in rivers and lakes (Bevanger, 2015). The ecological niche of mink and otter overlap to some degree, making them potential competitors (Bonesi et al., 2004). It is believed that the otter is the dominant competitor of the two because the body to weight ratio of otter and mink is about 7:1 and the otter is better adapted to hunting underwater (Bonesi et al., 2004). Studies have shown that at high densities of otters, mink shifts its diet towards more terrestrial prey due to competition for prey and intraguild predation (Bonesi & Macdonald, 2004). Hence, otters can be a factor for controlling mink populations in both aquatic and terrestrial habitat if terrestrial prey is not abundant (Bonesi et al., 2004).

In freshwater systems, salmonids such as Atlantic salmon and brown trout are common prey of both mink and otter (Erlinge, 1969; Heggenes & Borgstrøm, 1988). Previous studies have shown that fish mortality due to mink predation is greater in smaller tributaries with lower discharge, thus making predation risk greater for fish that are located in the smaller tributaries compared to those in the main river (Burgess, 1985; Heggenes & Borgstrøm, 1988). While salmon typically spawn in the larger river sections, trout (both anadromous and resident) normally spawn in the smaller tributaries and creeks (Reitaas, 2019). The anadromous trout (hereafter sea trout) population in the Trondheim fjord is currently at a historically low level (Bergan, 2013). Loss of spawning habitats, reduced access (i.e., barriers) to spawning habitat, and poor water quality are some of the reasons for the drastic population decline of sea trout (Bergan, 2013). However, mink predation may also be an important additive factor that explains the poor status of the sea trout population in Trøndelag and Norway in general (Heggenes & Borgstrøm, 1988).

Habitat selection of both mink and otter are affected by numerous factors (e.g., habitat characteristics and prey availability) (Dubuc, Krohn, & Owen Jr, 1990; Holland, Schauber, Nielsen, & Hellgren, 2019). As of today, it is not known to what extent these factors affect their distribution in the landscape simultaneously or if mink and otter occupy the entire range of a watercourse simultaneously. Salmonids, specifically Atlantic salmon and brown trout are the most abundant fish species in many watercourses of central and northern Norway. Both species have their own habitat preferences (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003). For example, salmon prefers sections of the river where the water velocity is slightly higher compared to trout (Armstrong et al., 2003; Louhi, Mäki-Petäys, & Erkinaro, 2008). As mink generally seem to select for slower flowing water, mink and trout may prefer similar areas. Anthropogenic disturbance such as agriculture, logging, and urbanization (i.e., roads, houses, etc.) are known factors that could impact ecosystems negatively, both on land and in water (Ojima, Galvin, & Turner, 1994; Yan et al., 2016). Both mink and otter are sensitive to changes in the lower trophic levels and to changes in the nearby land use, as well as to pollution and deterioration in water quality due to urbanization and agriculture (Holland et al., 2019; Melquist, Polechla Jr, & Toweill, 2003). To assess which variables govern the spatial distribution of mink in a watercourse, it is important to implement a holistic approach by simultaneously assessing to what extent terrestrial and aquatic habitat variables, availability of focal prey, and the community of potential competitors (e.g., otter) affect the distribution of mink.

The aim of this study was to investigate which factors influence the spatial distribution of the mink in a riparian landscape in Central Norway. To do so, I modelled the occurrence (biweekly at observation spots) of mink across the study system in relation to 1) sympatric vertebrate species (including potential prey, predators, and competitors), 2) habitat characteristics (both terrestrial and aquatic), and 3) the relative density of their main prey (salmon and trout). I predict that i) the presence of otters reduces mink abundance and that ii) water velocity and river width will be the most important habitat factors influencing the spatial distribution of mink. I predict that iii) mink observations occur more frequent in tributaries which contains high densities of salmonids and especially trout.

To investigate if otters are mainly connected to coastal areas, I modelled the occurrence of otter in the watercourse in relation to 4) the distance to the ocean and 5) the distance to the main river. I predict that iv) the detection rate of otters decreases with increasing distance to the ocean and v) that the detection rate of otters decreases with increasing distance to the main river.

This study represents a novelty in invasive species ecology research in Scandinavia by applying multiple dimensions in the search for explanatory variables that predict mink distribution in a riverine ecosystem. Most studies trying to explain mink distribution usually constrict to one, or two set of dimensions (e.g. habitat characteristics or prey availability) (Melero, Palazón, Revilla, Martelo, & Gosàlbez, 2008; Yamaguchi, Rushton, & Macdonald, 2003). The result will contribute to a better and more adaptive management of invasive mammalian species like mink.

2. Materials and method

2.1 Study area

The study area comprises the Figga watercourse in Steinkjer municipality, located in Central Norway (Figga watercourse, EU89 UTM 32 7094960 624518; Figure 1.). The main river Figgja flows North-West from the lake Leksdalsvatnet (68 MASL) and runs out in the Beitstadfjord. Historically, Figgja was a good river for fishing salmon. In 1977 the river was closed for fishing due to the discovery of the fish parasite *Gyrodactylus salaris*. Figgja has been subject to several rotenone treatments over the years to remove the parasite from the river system. The first treatment occurred in 1993 and the last one was carried out in 2009. Figgja was officially announced to be recovered in the autumn of 2014 and fishing started again in July 2015 (Steinkjerleksikonet, n.d.). Three main tributaries enter Figgja: Fløra, Skjelja and Døla. The smallest tributary, Fløra, flows out from Ålbergstjønna (86 MASL) and flows North-East before connecting to Figgja. According to previous reports, the upper parts of Fløra is without fish due to a barrier (a culvert) under the Norwegian County Road 6958 (Bergan, 2012). Skjelja, flows out from Buåstjønna (132 MASL) and flows North-East before it connects with Figgja. Døla, flows out from Henningvatnet (321 MASL) and flows North-West, then South-West before it connects with Figgja. Since 2011, there has been a hydropower plant in the upper part of Døla (NVE, n.d.). The region has a continental climate with an average temperature of 11.6 °C (May-Oct.) and -0.2 °C (Nov.-Apr.), and the average annual precipitation is 880 millimeters (Yr.no, n.d.).

Figure 1. Map showing the study area and its location in Central Norway. The Figga watercourse is highlighted in dark blue.

2.2 Camera trapping

To assess the relative presence/-absence (i.e., over discrete time window of 14 days) of mink, otter, and other mesopredators (e.g., red fox *Vulpes Vulpes* and pine marten *Martes martes*) in the landscape, we chose to use baited camera traps. Camera trapping is inexpensive compared to the use of personnel for monitoring sites continuously (Rovero & Zimmermann, 2016). Camera trapping is widely used in ecological studies to assess presence, abundance, and densities of species (Rovero & Zimmermann, 2016). To create a discrete study area, I used detailed land resource map (FKB-AR5, Norwegian Mapping Authority, Geovekst) of the Figga watercourse and added a buffer of 2 meters inland, around the shoreline. This was done because mink are closely linked to the shorelines and river banks (Hagström et al., 2011). Then, 210 points (200 focal points and 10 spare points in case a focal point could not be monitored, for example due to flooding) were randomly generated within this buffer area.

From the beginning of May 2019, 10 cameras were installed at a random location (referred to as camera sites) and relocated to a new random location after 14 days. If two camera sites within

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a 14-day period happened to be located within 500 m from each other, a new camera site was selected. This was done to reduce the chance of detecting the same mink at two active camera sites within the same period (i.e., autocorrelation or pseudoreplication). Melero et al. (2008) found that linear core area of mink was between 210-540 m and that core area of different mink not overlapped. Ideally, the distance between two active camera sites should be 1 kilometer but due to the limited size of the study area this was not possible. During the period of May 2019 to January 2020, 163 sites were monitored for 14 days (± 1 day) each, with motion triggered cameras equipped with passive infrared sensors (Browning Spec Ops Full HD, Browning Trail Cameras, Morgan, UT). Giving a total of over 2250 camera trap days. All cameras were set to take 3 pictures after motion detection with a 30 second delay between sequences. When configurating the pictures, all sequences with less than 2 minutes apart were considered as one sequence. To increase the detection probability of mink on a camera, we used a scent lure (Mink Gland Lure, Kishel's Animal Scents & Lures, East Aurora, NY). The lure comprised of a cotton swab impregnated with mink gland extract and mounted on a 25-30-centimetre wooden stick. The stick was planted in the ground (or snow) in front of the camera (range 60-320 cm) and centered in the middle of the picture frame. The use of attractants and especially scent lures are widely used in camera trap studies (Braczkowski et al., 2016; Bridges, Vaughan, & Klenzendorf, 2004; Moruzzi, Fuller, DeGraaf, Brooks, & Li, 2002). Cameras were mounted to the nearest tree from the random focal point coordinate (hereafter referred to as the zero-point). Both the horizontal and vertical angle of the cameras were measured. If a camera was pointed straight forward the horizontal angle was 0 degrees, if a camera was pointing downwards, positive degrees were added, and negative degrees if pointing upwards. Horizontal angle was set according to if a camera was pointing against the river or away, pointing directly against the river were set to 0 degrees. Camera height was measured from the ground and to the basis of the camera. Distance from the camera to the stick and distance from the camera to the water was also measured. All measurements were performed in centimeters. These measurements were done to control for the effective field of view in the statistical analysis. All spatial analyses (study design and data pre-processing) were conducted in ArcGIS Pro (Environmental Systems Research Institute (ESRI), 2019).

2.3 Habitat assessment

Habitat characteristics for inclusions as potential explanatory variables in the study were chosen based on literature (Holland et al., 2019; Previtali, Cassini, & Macdonald, 1998) and through discussions within the research group. I divided the habitat assessment into riverbank and river characteristics (i.e., terrestrial and aquatic habitat variables). Habitat assessments were carried out for all 210 points. Habitat assessment were always carried out by a team of two for safety reasons.

2.3.1 Riverbank characteristics

Bank height was defined as the height from the water level to the point where the end of a one-meter long ruler was perpendicular to the water surface (i.e., one meter inland). Bank type was categorized into two groups: gradual and discrete. A gradual bank type indicates a gentle slope whereas a discrete bank type indicates a steep, near vertical slope. Both were subjectively assessed within the margins of the bank height. Bank substrate was divided into four groups (i.e., rock, sand, pebbles, and vegetation) and one class containing "other". Bank substrate was subjectively assessed based on the most dominant (more than $1/3^{rd}$ of the area covered) substrate within the plot (10 m to each side of the zero point and approximately 2 m in width). To describe the vegetation (ground and field cover and tree layer), I considered 11 vegetation types and registered their presence/absence within the 10-m radius of the zero point. The vegetation classes comprised ferns/horsetails, graminoids, herbaceous plants, field shrubs, bryophytes/lichens, juniper, *Salix* sp./multi-stem trees, *Rubus* sp., pine, spruce, and deciduous trees. I summed up the presence (1) / absence (0) for all plots as an index for vegetation complexity at each site (i.e., 0 = indicate no vegetation at all, 11 = maximum complexity, presence of all vegetation types. I counted the number of stems within the same 10-m radius, as a measure of stem density. To measure the basal area of the forest, I used a relascope. The basal area of a forest is defined as the total cross-sectional area of all stems in a stand measured at chest height (Mitchell & Popovich, 1997). Canopy openness was defined as the proportion of the entire sky hemisphere that is unobstructed by vegetation when viewed from a single point (Jennings, Brown, & Sheil, 1999). Canopy openness was measured with a densiometer (Forestry Suppliers Spherical Crown Densiometer, Concave Model C) in all four cardinal directions and averaged. To obtain a measure of curvature of the river or creek, we measured the angle between the up and downstream 5 m from the zero point. If the river runs straight with the land for these 10 m, the angle was set to 180°. A convex curvature is represented when

the angle was below 180°, and a concave curvature occurred when this angle was greater than 180°. Tree trunks and debris from trees are a normal part of the river and forest habitat. We recorded presence/absence of deadwood in the water and on land for 10 meter up and downstream from the zero point in the river, and within a 10-m radius from the zero point on land. Main land use is a rough classification based on the most dominant landscape types in the nearby area. I defined the main land use based on what we observed standing in the zero point and about 100 m in each cardinal direction. If a 100-m line of sight was not possible, a geographical information system (GIS) was used to define the main land use. The categories of main land use are coniferous forest (CF), deciduous forest (DF), mixed forest (MF), agriculture (AG), pasture (PA), sub-urban (SU), urban (UR), felled area (FA), scrub land (SC), shrub land (SH), tall ferns (TF), tall grass (TG), wetland (WE) and flood land (FL). Distance to the main river and distance to the ocean was calculated for each site using network analysis in a GIS. Network Analysis is based on the mathematical sub-disciplines of graph theory and topology. The Figga watercourse was used as a network analysis layer and the shortest path analysis were conducted, calculating the distance (m) from each site to the main river and to the ocean.

2.3.2 River characteristics

River characteristics refer to the physical properties of the river and do not include chemical properties. The dimensions of the river were measured either by measuring tape, ruler, or with a laser rangefinder (1 m accuracy). Width (m) was measured between two points where the water meets the bank, across the river, and perpendicular to each other. Depth (cm) was measured two meters from the bank, or in the middle of the river when the river width was less than 4 m. Due to safety reasons and difficulty with measuring deeper depths, a maximum of 100 cm was used. For both width and depth, measurements were done at three places. One straight in front of the zero point and once at both the extremes of the zero-point along the bank. To assess the curvature of the river, we measured the distance between the extremes in a straight line. Distances close to 20 m indicate a straight flow, and the smaller distances indicate increased meandering. Water velocity was measured using a float. We recorded the time it took for the float to drift one meter downstream, three times per plot, and averaged drifting time to calculate surface velocity. Due to the different velocities and stream characteristics, we decided to go with only one meter for the velocity test, thus giving a coarse result. We chose the most representative place in the river to measure the water surface velocity. The riverbed substrate was assessed the same way as the bank substrate, subjectively, and as the most dominant

substrate within the plot. The riverbed substrate comprised five categories: sand (<1,9 mm grains), gravel (2-4 mm), pebbles (5-59 mm), cobble (60-200 mm), and boulder (+200 mm). In addition to the riverbed substrate, we also registered if there was aquatic vegetation present (covering at least 1/3rd of the plot) or absent in the river. Aquatic vegetation was defined as aquatic plants, submerged macrophytes, and periphytic algae.

2.4 Electro-fishing

Sixty sites were chosen randomly from 104 premade randomly chosen camera sites in Fløra (n = 11), Skjelja (n = 55), and Døla (n = 38) for camera trapping. In total, 47 of 60 sites were electro fished during the fall of 2019. The main river (Figgja) was not included in the electro-fishing (hereafter el-fishing) because the project's main focus is the sea trout, which usually spawns in the smaller tributaries (Aarestrup & Jepsen, 1998; Campbell, 1977). For estimating the density of salmonids, we intended to use the Zippin method (Zippin, 1958), even though it is known to systematically underestimate fish densities (Sandlund et al., 2005). The Zippin method is less invasive for captured fish than the more popular Peterson method, which is based on capture-mark-recapture techniques in which marking is usually done by clipping the adipose fin (Pine, Pollock, Hightower, Kwak, & Rice, 2003). Stunning fish with electric current causes stress and can inflict pain (Huntingford et al., 2006). Utilizing the Zippin method, fish are only stunned once. Using the Person method, fish risks to be stunned multiple times. Also, clipping the adipose fin inflicts unnecessary pain and increases stress (Mesa & Schreck, 1989). Hence, for animal welfare reasons, we opted for the Zippin method which is based on depletion rates between consecutive rounds of el-fishing (Bohlin, Hamrin, Heggberget, Rasmussen, & Saltveit, 1989). As a proxy for fish density, I standardized the total number of caught fish per 100m^2 for each plot.

All el-fishing was conducted by a team of two trained personnel. Permission for el-fishing was applied and granted by the County Governor of Trøndelag, before el-fishing began. The permit followed one specific person, which also had the responsibility that the el-fishing procedure went as planned. We fished each plot three times with 30 minutes between rounds, always starting downstream and moving upstream. El-fishing procedures were conducted the same way during the three rounds, normally zigzagging back and forth and never stepping into areas that were not yet fished. The transect fished was always 20 m long regardless of the river's width, meaning that the total area fished per plot varied (47.2 – 224.4 m^2). The zero point marked the middle of the transect. We used the electric fishing apparatus TERIK model FA-50 where the

working voltage is adjusted automatically at the beginning of the fishing based on the conductivity of the water. The purpose of this function is to achieve optimal efficiency in terms of conductivity. In low conductivity water, the device will automatically select a high voltage and vice versa. In some periods we used two teams and then another apparatus (TERIK model FA-40) was in operation. When using the FA-40, the voltage had to be adjusted manually. To ensure the correct amount of voltage, conductivity in the water had to be measured first using a conductivity meter (Model: CD-4307SD, Lutron Electronic Enterprise Co., Ltd.). The person who carried the apparatus was also in charge of the anode (which stuns the fish) and was equipped with one landing net. The person besides him was equipped with a landing net and was responsible for the bucket containing the captured fish. After each round the fish was identified and the length (i.e., total length) was measured in centimeters. The captured fish remained in their respective buckets until all three rounds of fishing were over. Water was changed whenever needed.

2.5 Data exploration and processing

All pre-processing of the data was conducted in Microsoft Excel prior to the statistical analysis, which was carried out in R software (3.5.1) via the RStudio (1.2.5033) interface (R Core Team, 2020). Data used in this analysis consisted of relative absence/-presence data from game cameras, fish density data, and habitat variables (measured or categorized in field or by using a GIS). For simplification of complex data and issues with data deficiency in the statistical analysis, several species registered with the camera traps were divided into functional groups as follows. 1) passerines, 2) ground nesters, and 3) Anseriformes (Table A1, appendix A). The fourth group, 4) *Rodentia* was created due to the difficulty of identifying small rodents on game camera photographs.

The two habitat variables 'pine' and 'juniper' were removed prior to the statistical analysis due to singularities in 'pine' and no observations of 'juniper'. The variable 'bank substrate' was removed because of few observations in three of the four categories. Likewise, the coarse scaled 'land use' variable was discarded because of issues with converge (i.e., the variables had extreme standard error values) and singularities. All numerical variables were checked for collinearity by using Pearson product-moment correlation coefficient. Dormann et al. (2013) argued that a correlation coefficient above 0.7 was an appropriate indicator for when collinearity severely distorts model estimation and affects predictions. I chose a more conservative correlation coefficient and opted for those variables with a coefficient above 0.6

to be discarded. The habitat variable 'canopy openness' and 'stems per 5 m' were moderate negatively correlated ($r(138)$ = -0.59). 'Canopy openness' was also negatively correlated with the habitat variable 'relascope' ($r(138)$ = -0.68). The two GIS derived variables distance to ocean and distance to the main river were highly correlated ($r(138)$ = 0.77). I chose to discard the habitat variable 'stems per 5 m' even though it is borderline the cut-off value. I also discarded 'relascope' and kept 'canopy openness' since this variable is most used of the three in other studies on the subject of mink habitat (Loukmas & Halbrook, 2001; Previtali et al., 1998). Of the two GIS derived variables, I chose to keep 'distance to the ocean' because this variable had more unique values for all data points while 'distance to the main river' contains many zeroes (n = 65) because some data points were located in the main river. Numerical variables were checked for outliers using boxplots and all outliers detected were considered as natural variation in the data set. Last, some rows were excluded from the dataset because of missing data (*NA's*).

2.6 Ordination analysis

An ordination analysis was conducted to investigate patterns in the vertebrate species composition matrix (i.e., camera trapping data) in our study system, and to identify environmental variables that explain part of that structure. I chose to use non-metric multidimensional scaling (NMDS) as ordination method because with NMDS you may use rank orders instead of Euclidean distances like in other ordination techniques such as Principal Coordinates Analysis (PCA). This makes NMDS more flexible in terms of what type of data it can accommodate. NMDS is run with the function *metaMDS* in the *Vegan* package (Oksanen et al., 2019) in R and is generally advised to run in parallel with another ordination method (Detrended Correspondence Analysis, DCA) as validation (van Son & Halvorsen, 2014). Before conducting the ordination, all birds besides of Heron (*Ardea cinera*) were grouped together in the following groups: 'passerines', 'ground nesters', and 'Anseriformes'. All other sympatric terrestrial species were included in the ordination except for two mustelid species (i.e., the stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*), which were grouped together as 'Small mustelids' (Table A1)). Grouping was needed to overcome data deficiency issues (e.g., species with rare occurrence are difficult to fit in an ordination). MetaMDS was run on the vertebrate species composition matrix (i.e., camera trapping data). Indices in Vegan are quantitative, so I used the argument '*binary* = TRUE' to make them presence/absence. The Jaccard distance for binary data (presence/absence) was applied for generating the distance

matrices. The Jaccard index, or the Jaccard similarity coefficient is used to measure similarity and diversity in sample sets (Jaccard, 1901). Data were fitted to 4 axes (i.e., 4 dimensions) to ensure low stress values (a low stress value indicates a high goodness of fit). A stress plot and the R^2 values were used to assess model robustness. I used a minimum of 50 and a maximum of 100 random starts in search of a stable solution. After 50 random starts has been reached, the iteration stops when two convergent solutions are found or when 100 random starts are reached. Due to many zeros (i.e., few observations of different species at each plot) in the species matrix, I used the *noshare* argument in the NMDS analysis. When 'noshare' is called for, the function 'stepacross' is used when the proportion of site pairs with no shared species exceeds the value of 'noshare' (Oksanen et al., 2019). Noshare was set to 0.1. The stepacross function attempts to replace dissimilarities with a shorter path, stepping across intermediate sites. Dissimilarities above a certain threshold are considered as missing data (*NA*). Implementation of 'noshare' should improve the ordination with high beta diversity when there are few species and many sites with no species in common (Oksanen et al., 2019). I used the 'envfit' function to link the environmental variables to the species ordination and used a permutation test with 999 iterations to identify variables with a significant impact on the species community structure. I chose $\alpha = 0.05$ as a threshold for statistical significance in all statistical analysis. As a validation for the NMDS I conducted a DCA. I used DCA instead of ordinary correspondence analysis (CA) to overcome the distortions inherent to basic correspondence analysis ordination (Hill & Gauch, 1980). Detrended correspondence analysis was carried out with the *decorana* function in the *Vegan* package in R. Additionally, I used the *iweight* argument when running the DCA. When 'iweight' is called for, down weighting of rare species is applied.

2.7 Univariate analysis

Logistic regression was used to assess the probability of detecting mink (0 = no detection, 1 = detection; the response variable) in relation to the presence/absence of sympatric vertebrate species (potential prey, predators, and competitors) (Table A2) and in relation to the relative density of salmon and trout per 100 m^2 and habitat characteristics (aquatic and terrestrial) (Table A3). Generalized linear models (GLM) were fitted to the data with a binomial error distribution since the response variable mink was binary. No interactions between explanatory variables were considered in the regression analysis because the result of interactions between multiple independent variables are challenging to interpret and to avoid overfitting the models. Model selection was done using the Akaike Information Criterion (AIC) corrected for small sample

sizes (i.e., AICc), to rank the competing models and to weight the relative support for each model (Akaike, 1973; Johnson & Omland, 2004). Due to the large number of explanatory variables used (n = 39), model selection based on all variables simultaneously was not possible (n = 2^{39} different model combinations). Therefore, I first determined informative variables based on a set of 'topical' models: i.e. mink detection probability in relation to 1) competitor presence-, 2) prey presence-, 3) presence of other sympatric species-, 4) terrestrial habitat characteristics-, and 5) aquatic habitat characteristics. I used the dredge function from the *MuMIn* package (Barton, 2019) in R to generate a model selection table including all possible model structures based on the variables in the full model of each topical model. The most simple model, within the range of ΔAICc < 2 was selected as being the most parsimonious topical model (Blumer, Ehrenfeucht, Haussler, & Warmuth, 1987). ΔAICc is the difference between the AICc value of a candidate model and the AICc value of the best ranked model, models having ΔAICc ≤ 2 have substantial support (Burnham & Anderson, 2004). In the second step, I included all model terms retained in the most parsimonious topical models in a global model and repeated the model selection procedure as described above. I used residual deviance divided by the degrees of freedom to evaluate the dispersion of the final model.

The fish density data was analyzed separately as this only comprised 36 records. Here I fitted the variables density of salmon per 100 m^2 and the density of trout per 100 m^2 to a GLM to investigate if fish density affects the detection rate of mink. There were not enough observations to include river ID as an interaction to check for differences between tributaries. Dredging was used to test all possible model structures and the model with least parameters within the range of ΔAICc 0 – 2 was selected as the best fit model. Residual deviance over degrees of freedom was used to validate the final 'best fit' model.

To assess the probability of detecting otter in relation to the distance from the ocean and the distance from the main river I used the same procedure as before, fitting a GLM to the data and by using dredge to generate a model selection table including all possible model structures. Model selection and validation was executed as described above.

3. Results

163 of 210 sites had cameras deployed during the period 1 May 2019 to 17 January 2020. 141 of 163 camera sites were used in the analysis (140 in the ordination analysis due to no species at one site), whereas 22 were discarded because of malfunctions, improper setup, or no data. The remaining 141 camera sites were distributed across the different rivers as follows: Figgja, 65; Skjelja, 39; Døla, 28; and Fløra, 9. Mink was detected at 22.7 % of the camera sites (n = 32): Figgja, 19; Skjelja, 9; Døla, 3; and Fløra, 1. Whereas otter appeared at 31.9 % (n = 45): Figgja, 29; Skjelja, 10; Døla, 3; and Fløra, 3. Fifty-seven different vertebrate species were observed in total at the camera sites, in addition to small rodents (33.3 %, n = 47 sites). Of the 57 vertebrate species, 43 were included in the analysis, plus rodents. For more information on species observations see Table A1 and Table A2. Of the functional groups, passerines were observed at 61 % (n = 86) of the sites, ground nesters at 7.1 % (n = 10) of the sites, and Anseriformes at 8.5 % (n = 12) of the sites. Forty-seven (22.4 %) of the 210 sites were el-fished during autumn 2019, 36 of them corresponded with the 141 camera sites. In total of 2053 (mean 43.7) fish were caught during el-fishing: 741 (36.1 %) salmon, 1257 (61.2 %) trout and 55 (2.7 %) three-spined sticklebacks (*Gasterosteus aculeatus*). The mean density of trout per 100 m^2 in the different tributaries was as follows: Skjelja, 39.52; Døla, 15.23; and Fløra, 7.82. The mean density of salmon per 100 m^2 in the different tributaries was as follows: Skjelja, 13.57; Døla, 19.32; and Fløra, 1.66. Mink was detected at 13.9 % of the 36 fished sites.

3.1 Ordination analysis

The NMDS analysis shows how the species composition relates to the camera sites (Figure 2). Here we see that mink is closely associated with prey species like passerines and ground nesters as well as with pine marten. The otter is more closely associated with other small mustelids than with mink. Surprisingly, no predators were associated with small rodents like mice and voles. The low stress value of 0.12 (and non-metric fit, $R^2 = 0.986$) indicates a good fit of the NMDS model (Figure B1, appendix B). Of the environmental variables, *Salix* sp. ($r^2 = 0.0224$, p = 0.044), *Rubus* sp. ($r^2 = 0.0240$, p = 0.035), spruce ($r^2 = 0.0278$, p = 0.018), and bank height ($r^2 = 0.0202$, p = 0.049) significantly impacted the species community structure (Figure 2).

The DCA was run as a validation to the NMDS and showed that mink was associated with prey species like passerines but indicated a greater distance to ground nesters and pine marten (Figure B2). The NMDS and the DCA generally produced similar results, except that small

mustelids showed a far greater distance from other species in the DCA plot compared to the NMDS.
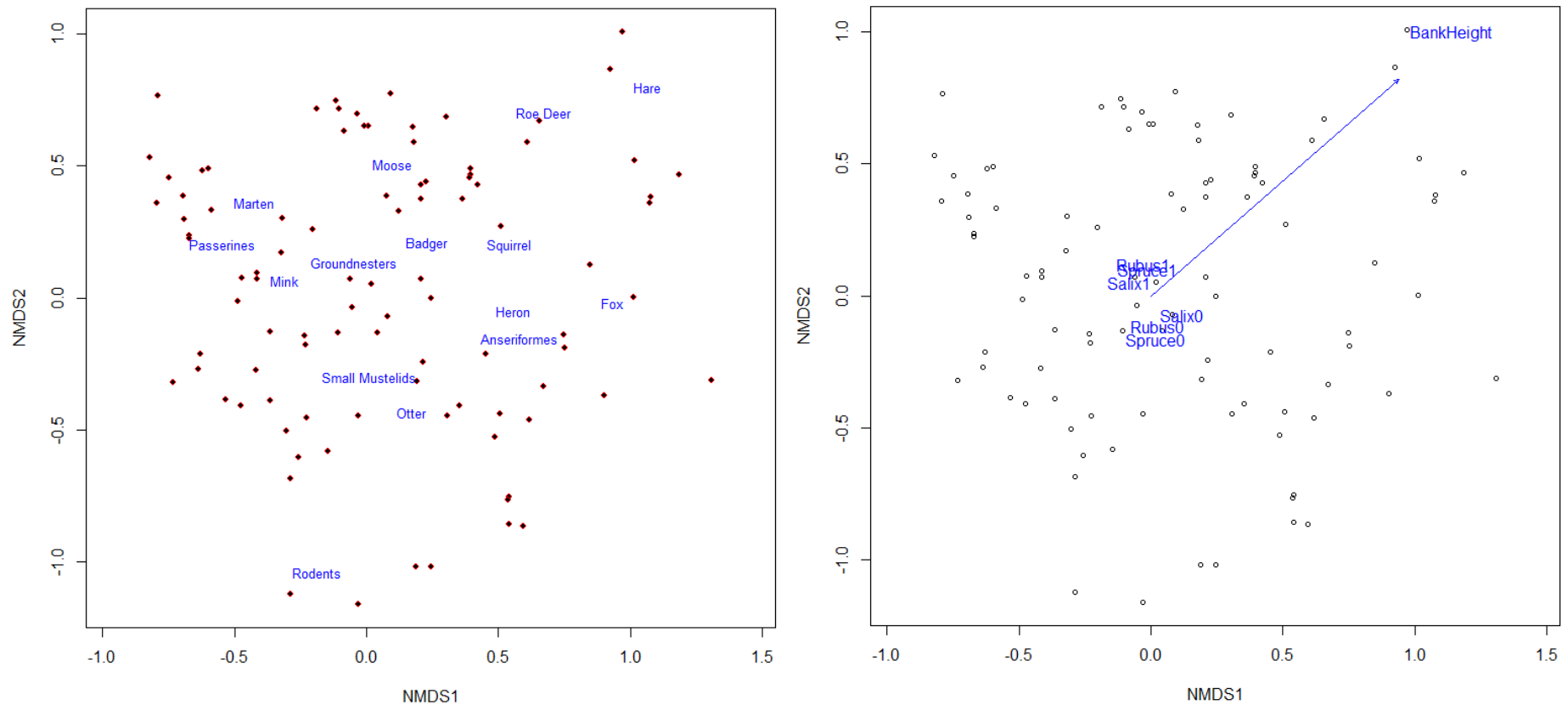
Figure 2. NMDS plot showing how species are associated to each other and to the camera sites (red dots) (left panel). Habitat variables with significant impact on the species community structure (right panel). The ordination plot shows that mink was closely associated to passerines, ground nesters, and pine marten. It shows that mink was more associated to sites with presence of spruce, *Rubus* sp., and *Salix* sp., than places without, and was more frequently observed at sites with lower bank heights.

3.2 Factors affecting mink detection

The competition model was modelled as a function of relative presence/-absence of mink against observed species which are known competitors of mink or have similar diet or show similar habitat use. The full model included presence/absence of otter, pine marten, badger (*Meles meles*), red fox, stoat, and least weasel as explanatory variables. Out of all possible model combinations, four candidate models were within the range of ΔAICc 0 – 2. The most parsimonious model only included presence/absence of pine marten (ΔAICc = 0.48, w_i = 0.245, residual deviance: 145.32 on 139 df) but I acknowledge that the other models might have been important since their AIC weight (w_i) was similar compared to the most parsimonious model (Table C1, appendix C). However, I only retained presence/absence of pine marten for the second step of the analysis.

The prey model was modelled as a function of relative presence/-absence of mink, against observed presence/absence of mink prey species divided into functional groups, with the full model including passerines, ground nesters, Anseriformes, hares (*Lepus timidus*) and other rodents. After running all possible model combinations based on the full model, the most parsimonious model within the range of ΔAICc 0 – 2 only included passerines as a predictor (ΔAICc = 0.70, w_i = 0.228, residual deviance: 140.53 on 139 df). Here as well, other candidate models had similar AIC weights compared to the most parsimonious one (Table C2). Passerines were included in all the candidate models within ΔAICc < 2. Hence, I only retained the presence/absence of passerines for the second step of the analysis.

The sympatric species model was modelled as a function of relative presence/-absence of mink, against observed presence/absence of species which are not considered as competitors nor prey of mink. The full model included Moose (*Alces alces*), Heron (*Ardea cinerea*), Roe deer (*Capreolus capreolus*), and Red squirrel (*Sciurus vulgaris*) as explanatory variables. After running all possible model combinations, the intercept-only model was ranked as the best model (Table C3). Hence, no sympatric species other than prey or competitors were included in the second step of the analysis.

For terrestrial habitat variables, the full model included bank type, bank height, canopy openness, distance to the ocean, and presence/absence of ferns/horsetail, graminoids, herbaceous, field shrub, bryophyte/lichens, *Salix* sp., *Rubus* sp., pine, spruce, deciduous, and deadwood as explanatory variables. After running all possible model combinations, 33 candidate models were included within a ΔAICc range of 0 – 2 (Table C4). The most

parsimonious model included the predictors: bank height and presence/absence of *Salix* sp. and spruce (ΔAICc = 1.18, w_i = 0.03, residual deviance: 133.62 on 137 df). These tree variables were retained and included in the second part of the analysis. Nevertheless, I am aware that other candidate models might have been important since their AIC weight (w_i) was similar compared to the most parsimonious model.

The aquatic full model for assessing detection probability of mink included the aquatic habitat variables river ID, land-water angle, average river width, average river depth, the distance between extremes, velocity, bottom substrate, and the presence/absence of deadwood in the river and aquatic vegetation. After running all model combinations, 14 candidate models were included within the ΔAICc range of 0 – 2 (Table C5). The intercept-only model was included in the 14 candidate models. Hence, no aquatic habitat variables were retained for further analysis.

Model selection based on the global model included 'pine marten' from the competition model, 'passerines' from the prey model, and 'bank height', '*Salix* sp.', and 'spruce' from the terrestrial habitat model (and no variables from other topical models), resulted in two candidate models with ΔAICc < 2 (Table C6). One of the models was the global model (ΔAICc = 0.19, w_i = 0.48, residual deviance: 126.56 on 136 df), whereas the most parsimonious model of the two did not include pine marten (ΔAICc = 0, w_i = 0.52, residual deviance: 128.52 on 137 df). Looking at parameter estimates of the final model both presence of passerines (Figure 3, estimate β = 1.46, standard error se = 0.54, p-value = 0.01) and spruce (Figure 4, β = 1.16, se = 0.51, p = 0.02) had a positive impact on the detection rate of mink, whereas bank height had a slightly negative impact (Figure 5, β = -0.02, se = 0.01, p = 0.01) on mink detection probability (Table D1, appendix D).
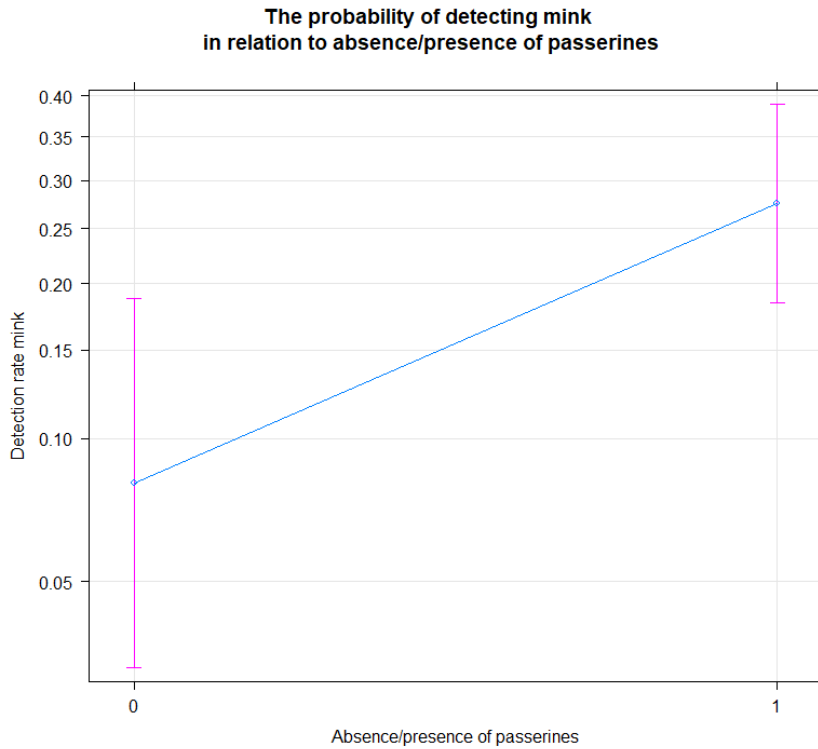
Figure 3. Predictor effect plot showing the predicted detection rate of mink when passerines are present or absent. The presence of passerines clearly increases the likelihood of detecting mink at the same camera site. The pink lines represent a 95 % confidence interval.
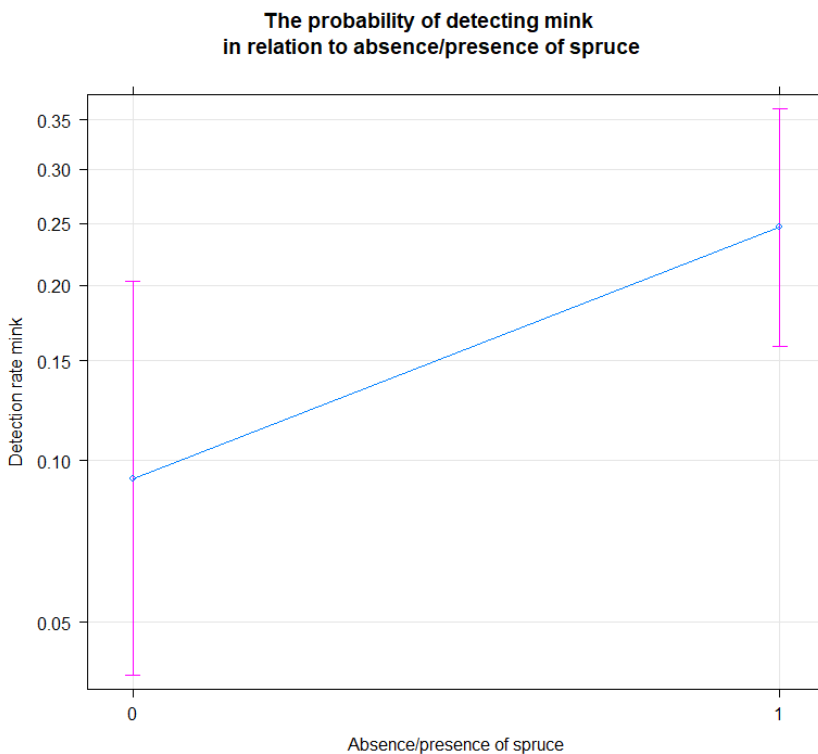
Figure 4. Predictor effect plot showing the predicted detection rate of mink when spruce is present or absent. The presence of spruce increases the chance of detecting mink. The pink lines represent a 95 % confidence interval.

Figure 5. Predictor effect plot showing the probability of detecting mink in relation to the height of the riverbank. Mink detection rate decreases with increasing bank height. The blue line is the regression line and the light blue area represents the 95 % confidence interval. The tick marks at the bottom represent all data points.

Linking relative presence/-absence of mink to salmonid density resulted in the most parsimonious model (i.e., ΔAICc = 0 and w_i = 1) with density of trout per 100 m^2 as the only predictor (residual deviance: 23.961 on 34 df) (Figure 6, Table C7). The density of trout had a borderline significant effect on mink detection rates (β = 0.04, se = 0.02, p = 0.08) (Table D2).

The probability of detecting mink
compared to the density of trout per 100m2
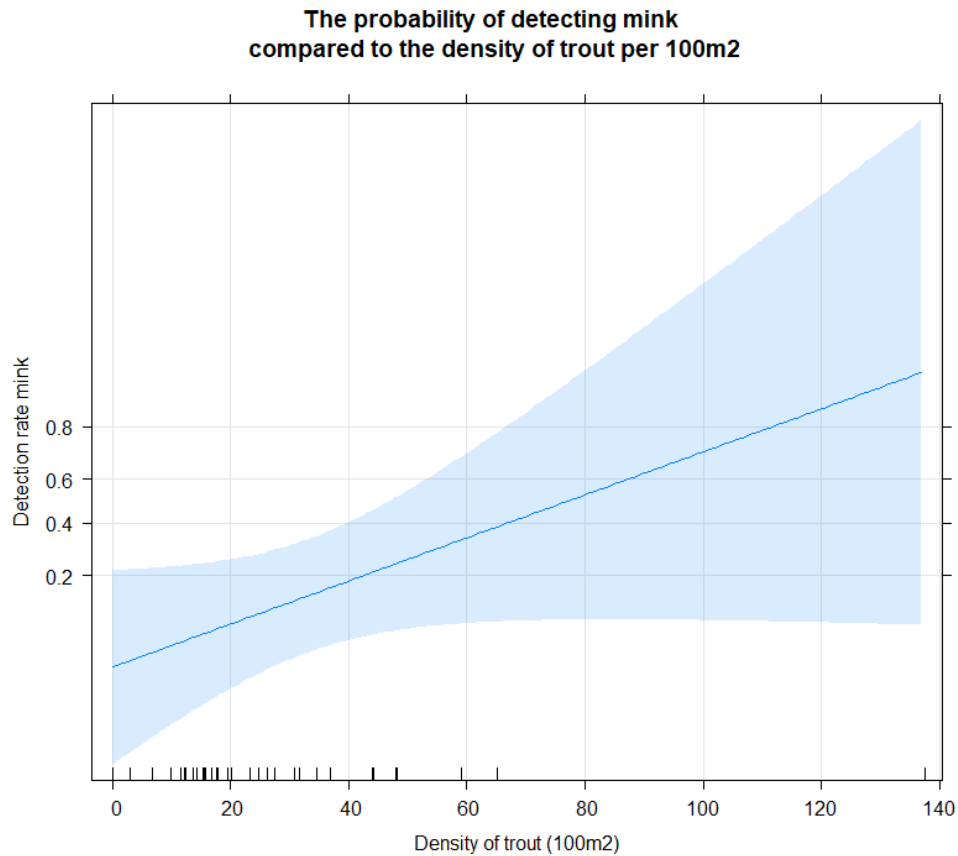
Figure 6. Predictor effect plot showing the probability of detecting mink in relation to the density of trout per 100 m^2 in the river. The blue line is the regression line and the light blue area represents the 95 % confidence interval. The rug plot at the bottom represent all data points. The width of the confidence interval is quite large at high densities due to only one 'observation' between 70 – 140 trout per 100 m^2.

3.3 Otter detection in relation to proximity to the ocean or the main river

Linking relative presence/-absence of otter to the distance from the ocean and the distance from the main river resulted in two candidate models within the range of ΔAICc 0 – 2 (Table C8). The most parsimonious model (ΔAICc = 0 and w_i = 0.674, residual deviance: 167.46 on 139 df) only included the variable 'distance to the ocean'. Otters were more frequently observed close to the ocean and the distance from the ocean had a significant negative effect on the likelihood of detecting otters (β = -0.10, se = 0.03, p < 0.001) (Figure 7, Table D3).
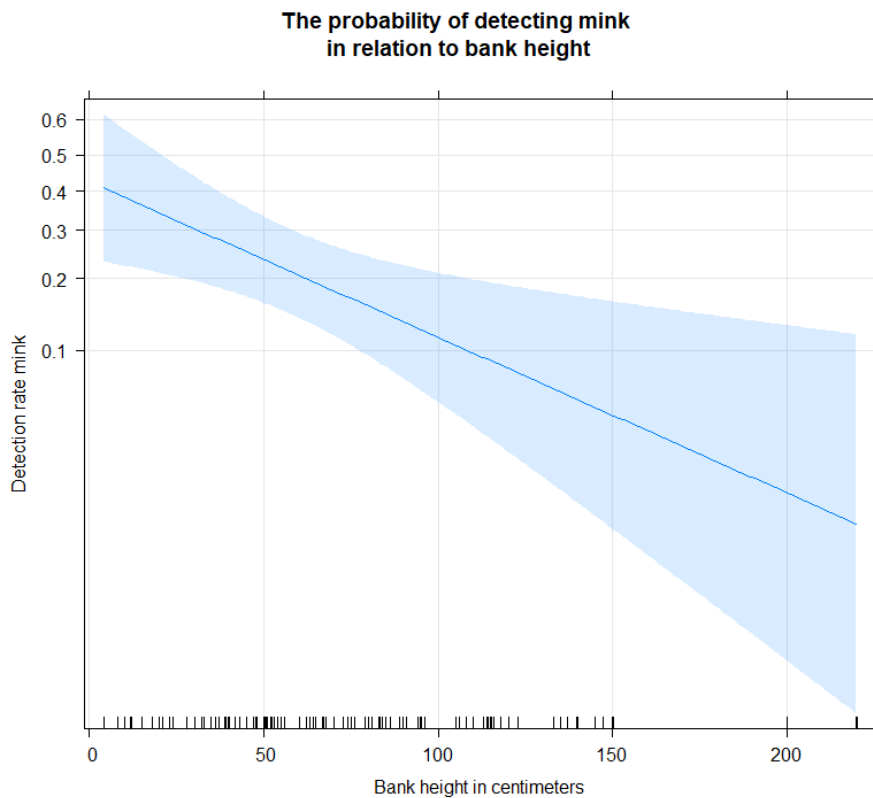
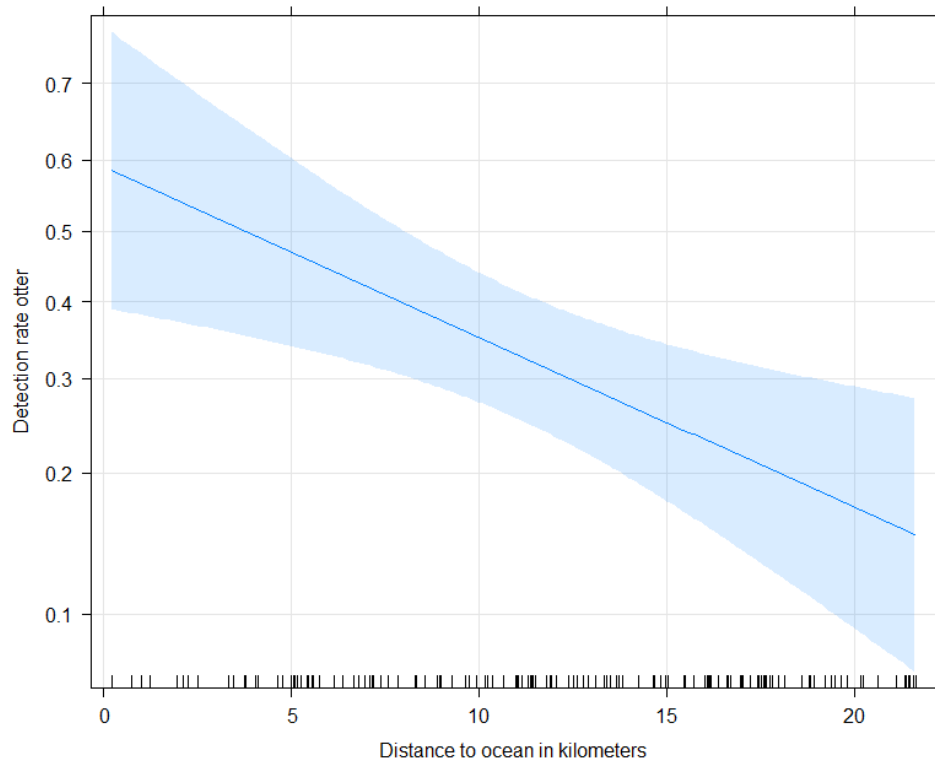**Figure 7.** Predictor effect plot showing the probability of detecting otters in relation to the distance from the ocean. Detection rate decreases with increasing distance from the ocean. The blue line is representing the regression line and the light blue area representing the 95 % confidence interval. The rug plot at the bottom represent all data points.

4. Discussion

This study did not find support for the prediction that the presence of otters reduces the likelihood of mink being present. Mink and otter observations occurred more often in the main river. However, out of the three tributaries, Skjelja had the most mink observations and the highest mean density of trout per 100 m^2. The prediction that mink occur more frequently in tributaries with high densities of trout was not confirmed (though borderline significant). Mink and otter observations followed the same pattern in terms of observations per river. This pattern corresponded very well to the mean density of salmonids per 100 m^2 in the tributaries and older catch statistics for Figgja (Holthe, Rikstad, Bjøru, & Larsen, 2017), indicating that higher density of salmonids were related to more observations of both otter and mink.

In the final model, only passerines out of the sympatric species had a significant (and positive) effect on the detection rate of mink. In terms of influential habitat variables, neither water velocity nor river width showed to be influential for mink detection likelihood. Instead, bank height and the presence of spruce showed a significant effect on the detection rate of mink. With increasing bank height, mink detection rates decreased, and the presence of spruce increased the likelihood of mink being present

The prediction that distance from the ocean affects otter detection was confirmed, with otters being more frequently detected closer to the ocean. However, distance from the main river had no significant impact on either mink or otter detectability.

As far as I know, my results of which factors affecting mink detectability has never been presented in a similar study. Though passerines have been reported as mink prey before, it constitutes only a small portion of the mink diet (Chanin & Linn, 1980). If my results are due to a more strict model selection procedure is difficult to say but there were many competing candidate models among the topical and global models within the range of ΔAICc 0 – 2, models that could contain substantial information (Burnham & Anderson, 2004). The three explanatory variables in the final model explained approximately 15 % of the variation in the model, suggesting that other variables (perhaps not measured) may affect mink detectability in the landscape.

4.1 Competitors

The competition model excluded otter as a potential explanatory variable and almost all other known competitors of mink. The prediction that the presence of otters reduces the likelihood of mink being present, was disproved. In contrast, mink and otter observations followed a similar pattern in terms of observations per river and mink observations occurred mostly in the main river (59.4 % of all observations). Mink and otter were observed at the same camera site within the same time-period at 14 different sites. This comprises 43.75 % of all mink observations and 31.11 % of all otter observations.

As mentioned before, apex predators can displace or outcompete mesopredators (Gordon et al., 2015). Nevertheless, the isoleg theory postulates that two competing species could coexist based on optimal foraging and differentiation in habitat selection (Pimm & Rosenzweig, 1981). Isoleg theory also predicts that coexistence is favored when one of the species is a specialist (especially the dominant one), while the other one is a generalist (Rosenzweig, 1987). When the specialist is also the dominant species, coexistence is predicted to be favored in areas with heterogeneous habitats, where the subordinate generalist can segregate from the dominant specialist (Bonesi & Macdonald, 2004).

For instance, the yellow-pine chipmunk (*Neotamias amoenus*), which is a generalist rodent living in the Rocky Mountains in Canada, coexists with two different rodent specialists through habitat differentiation (Morris, 1996). The North American deer mouse (*Peromyscus maniculatus*) favors xeric habitat (i.e., a dry environment), and the southern red-backed vole (*Myodes gapperi*) favors mesic habitat (i.e., a moderate moisture environment); the yellow-pine chipmunk can coexist with these two specialists by exploiting the margins of their preferences (i.e., by using a vacant or underused habitat) (Morris, 1996).

Another example is the prey body-size selection of leopard (*Panthera pardus*) and lion (*Panthera leo*) in the Bubye Valley Conservancy in the Republic of Zimbabwe. These two sympatric predators select prey of different body-size, regardless having access to the same species. Selection on different prey body size is believed to reduce competition between the leopard and the lion (Du Preez, Purdon, Trethowan, Macdonald, & Loveridge, 2017). Clode and Macdonald (1995), and Erlinge (1969) demonstrated this prey body size selection also in sympatric mink and otter: 30 % of the fish that was taken by otter exceeded the maximum size of fish usually taken by mink (Erlinge, 1969).

Bonesi and Macdonald (2004) demonstrated the isoleg theory in practice by showing that mink (the subordinate generalist) and otter (the dominant specialist) can coexist in areas with habitats where mink can segregate from otter. They also demonstrated that coexistence was favored in areas where terrestrial prey where likely to be more abundant. In addition, Bonesi and Macdonald (2004) argued that otter outcompeted mink in areas characterized by fewer mammalian prey and where broadleaf forests were the dominant habitat.

If we evaluate my result considering the isoleg theory, it could be that mink and otter do not display interference competition as a result of access to abundant terrestrial prey, e.g., passerines and the possibility for mink to segregate from the otter. In summary, the isoleg theory implies that coexistence of similar competitive species depends on their ability to share resources (i.e., resource partitioning) (Pimm & Rosenzweig, 1981) and can explain patterns found in this thesis.

As mentioned in the introduction, the otter population in Norway declined from the 1950s and onward (Heggberget, 1988; Tison et al., 2015). Since 1990 there has been an increase in the otter prevalence in Norway, but the true population size and distribution is still unknown (van Dijk, May, Hamre, & Solem, 2016). A new population decline also probably occurred in the period from 2006 to 2010 (van Dijk & May, 2012). When a specialist is maintained below their carrying capacity, it is believed to favor generalist species (Morris, 1996). In addition, dispersal limitation of specialists could give an advantage to generalists during colonization of new habitats (Büchi & Vuilleumier, 2014).

Pine marten was the only sympatric 'competitor' in the final competition model but was discarded in the last step of the analysis. I use the term 'competitor' because very little is known about the relationship between mink and pine marten (Hodder, Larsen, & Crowley, 2017). Previous studies have concluded with little or no competition between these two species (Powell & Zielinski, 1983). Assumptions were made that mink are more linked to aquatic habitats and that pine marten mostly consume terrestrial prey and therefore are more associated with terrestrial habitats (Powell & Zielinski, 1983). Kiseleva (2012) on the other hand, found that mink and pine marten had substantial niche overlap (coefficient 0.75 on a 0-1 scale) and that under normal conditions, resource partitioning was achieved due to spatial segregation.

4.2 Prey species

Mink distribution is known to be influenced by access to and availability of prey species (Holland et al., 2019; Yamaguchi et al., 2003), which my results also supports. 'Passerines' was the explanatory variable with the greatest effect on the detection rate of mink and was a functional group consisting of 25 different species and 1 genus (*Turdus*). Due to the great variety of birds in the group, it is difficult to say which species had the most impact on mink detection. The low number of some species occurrence made it impossible to do regression analysis on all passerine species. The genus *Turdus* with its four species, made up for more than half of the observations of passerines (see table A1).

Predation on passerines by mink has not received much attention in the field of research. Most studies have focused on the effects on waterfowl and ground nesters. Nevertheless, there are some that includes passerines as well (Arnold & Fritzell, 1987; Chanin & Linn, 1980; Nordström et al., 2003).

In North America, mink has been reported as a predator on marsh-nesting blackbirds (Icteridae) (Arnold & Fritzell, 1987). Though they are not related in any way, the common blackbird of Europe lays it nest either on the ground or near the ground in bushes or trees (Hatchwell, Chamberlain, & Perrins, 1996), and in that way, they are at risk for predation by mink. Common blackbird and other thrush species are the most common passerines of the study area.

Deciduous riparian habitats are often heterogenous with a complex vegetation structure (Capon & Dowe, 2007). These habitats are important resting places for migratory passerines and also to breeding birds (Stevens, Brown, Simpson, & Johnson, 1977). Stevens et al. (1977) found that migrant passerine density and migrant passerine species diversity was higher in heterogenous deciduous riparian habitats than in uniform stands of riparian growth. This could explain the high number of observations of passerines in the study area and hence the abundance of terrestrial prey.

There were not many observations of Anseriformes (n=12) or ground nesters (n=10) on the cameras, and most were observed while just passing by a camera site. Therefore, it is difficult to say if the result from the prey model showing that both presence of Anseriformes and ground nesters yielded non-significant for the likelihood of mink being present, is due to a low number of observations or because the presence of Anseriformes and ground nesters simply do not affect mink presence.

Fish consist of a large part of the minks' diet (Heggenes & Borgstrøm, 1988). Hence, it is a logical presumption that mink would occur more frequently where the fish is abundant, or in other words, that mink abundance fluctuates with fish density. Hodder et al. (2017) found that mink occupancy was higher in fish-bearing streams than in non-fish-bearing streams. My result did not find support for that prediction, although it was borderline. Mink presence was more related to the density of trout compared to the density of salmon or salmonids in total. A possible explanation for this could be that mink and trout prefer much of the same river characteristics: i.e., deeper and relatively slow running water (Heggenes, 1996; Macdonald & Harrington, 2003).

4.3 Habitat variables

Mink is a generalist in the broadest sense of the word, it utilizes a broad spectrum of prey and is capable of living in many different habitats (Arnold & Fritzell, 1990; Bonesi, Dunstone, & O'Connell, 2000; Previtali et al., 1998; Thierry, 1993; Yamaguchi et al., 2003). Riparian systems epitomize heterogeneity and contribute to high biodiversity, elevated biomass, and productivity (Naiman et al., 2005). Habitat heterogeneity (in space and time) tends to favor generalist species, not only because of the forage species richness but also the availability of hiding places (Büchi & Vuilleumier, 2014; Gundersen et al., 2010).

The detection rate of mink was positively affected by the presence of spruce and *Salix* sp. and deciduous trees (albeit the latter not significant) in the final model, contrary to other studies where mink presence has been shown to correlate positively with alder (*Alnus* sp.) and willow trees (*Salix* sp.), and negatively correlated with coniferous trees (Hodder et al., 2017; Mason & Macdonald, 1983; Melero et al., 2008). The ordination plot of the NMDS analysis provided evidence that presence of spruce and presence of *Salix* sp. are closely related, and both significantly affected the community structure of the observed species by the camera traps.

It is possible that these mixed habitats, contain a higher abundance of rodents and thus provide a resource to terrestrial prey. Also, spruce is the primary wood for logging in Norway (Fjellstad, 2017), meaning that there will always be a connection to clear cut areas in the proximity to large stands of spruce, especially around farmland. Felled areas are recognized to contain higher densities of small rodents (especially bank vole (*Myodes glareolus*) and yellow-necked mouse (*Apodemus flavicollis*)) but also support higher densities of small predators (Sidorovich,

Solovej, Sidorovich, & Rotenko, 2008). The bank vole is known as an important prey for mink, especially in proximity to otters (Bonesi et al., 2004).

Bank height was the only abiotic environmental factor that affected mink presence. Mink was generally detected at low bank heights (regardless of the characteristics of the bank type), and the detection rate rapidly declined with increasing bank height. The median bank height for sites with mink detection was 49 cm (range 8 – 135 cm, mean 55.28 cm). Sites not visited by mink were usually represented with a discrete bank type (n=71, 65 %) and a median bank height of 70 cm (range 4 – 220, mean 75.4 cm). A possible explanation for this could be that mink find it harder to go ashore on riverbanks characterized as discrete with heights exceeding 60 cm. Other studies have also reported that mink occur more often at river banks with a gentle slope (Strachan, Jefferies, Barreto, Macdonald, & Strachan, 1998).

4.4 Otter detection in relation to proximity to the ocean or the main river
Otters are known to be influenced by stream order and length, shoreline diversity, woodland cover, the influence of agriculture and pastures, and prey availability (Dubuc et al., 1990; Holland et al., 2019; Jeffress, Paukert, Sandercock, & Gipson, 2011; Jeffress, Paukert, Whittier, Sandercock, & Gipson, 2011). In this study, I only assessed 'distance from the ocean' and 'distance to the main river' as potential factors that affect otter presence. Looking at the distribution of observations, it seems that the otter is mainly linked to the main river (64.4 % of all observations), which is the highest order stream in the watercourse. The distance from the main river did not affect otter detectability. The distance from the ocean affected the distribution of otters, with increasing distance to the ocean, the likelihood of detecting otters decreased. This could possibly be a dispersal limitation for otters and could be an advantage for mink during colonization.

4.5 Limitations to the study and study design
Habitat assessment were carried out between the 11 July and 24 August and some habitat parameters varied during that period. The habitat assessment was only a snapshot of how explanatory variables appear at that moment in time. The fluctuations that occur throughout the year are not always evident. The amount of precipitation, level of groundwater, or the length of a drought, for example impacts the discharge, water velocity, and the depth in the watercourse. In addition, vegetation phenology cannot be captured using a snapshot approach. The lush

vegetation at the end of July is not there in early May or at the end of November. So, in conclusion, the presence of mink is only being compared to a snapshot of habitat variables, while the true conditions at the time of camera deployment may have been different. A solution to this could be to implement habitat assessment as a part of the camera setup to get as close the real conditions as possible and consider the precipitation relative to the amount of discharge in the river for each period.

One of the habitat variables expected to impact mink detection was land use. This variable was discarded after problems with model convergence and uncertainties about their assessment. The variable consisted out of 14 different land cover types. In retrospect, I acknowledge that I should have considered less characteristics, and perhaps determined land use by the help of orthophotos, classified satellite imagery, or spectral vegetation indices as a proxy for land use (e.g., Normalized Difference Vegetation Index (NDVI)) (Fisher, Acosta, Dennedy-Frank, Kroeger, & Boucher, 2018; Jeong, Mo, Kim, Park, & Lee, 2016; Szostak, Wezyk, & Tompalski, 2014).

During the fieldwork, signs of mink (i.e., tracks and scats) where found in parts of the tributaries which did not have any observations of mink on camera. The difference between observations of mink tracks and scats and observation of mink on camera could imply that the abundance of mink, was underestimated in some areas.

4.6 Implications of this research and adaptive management
The mink population in Norway is large and viable. It represents a threat because of the considerable negative impact it can have on native wildlife such as waterfowls and ground nesters, several of them endangered. From 2025, fur farming in Norway is prohibited (Landbruks- og matdepartementet, 2019). This means that the source of mink escapes into Norwegian nature will disappear, one hundred years after it first arrived. Although mink is difficult to remove, I advise designing trapping campaigns for mink that cover entire watercourses and take into account the variables pointing to the preferred areas in order to be more successful in the adaptive management of mink.

Moreover, traps should be placed near the river, preferably on riverbanks not higher than 50 cm. The results suggest that the probability of detecting mink on riverbanks higher than 50 cm is less than 20 %. Regarding habitat types, I would argue to focus trapping in areas of both spruce forest and heterogeneous deciduous habitats with elements of spruce even though spruce

was the only habitat variable representing vegetation in the final model. The fact that mink detection coincided with spruce trees does not mean that detection was done in a coniferous forest, merely that spruce was present at the camera site. Two-thirds of all mink observations occurred in either coniferous forest (n=9) or mixed forest (n=10).

As an experimental trail I would suggest to test floating rafts (i.e., mink rafts), equipped with traps (Reynolds, Short, & Leigh, 2004). Mink rafts could first be used to test if there are presence of mink by using a tracking cartridge (which consists of a basket, oasis foam and clay/sand mixture) inside a tunnel to record footprints (Reynolds et al., 2004). After mink has been detected, traps could be mounted. This is a good approach if there is a limited access to traps. Additional, either baits with small amounts of fish or scent lure in the form of mink gland could be used to attract mink, but the raft itself exploits the minks' natural curiosity, and rafts do not require baiting to attract mink (Reynolds et al., 2004; Roy, Macleod, & Moore, 2006).

5. Conclusion

This study shows that it is challenging to determine factors affecting the distribution of mink in a riparian landscape, and that the explanatory variables from the final model explained only about 15 % of the variation in the response variable 'mink', underpins this notion.

Otters have probably minimal effect on mink distribution in a heterogeneous riparian landscape, since the abundance of terrestrial prey is more sufficient in such areas and mink can segregate from the dominant otter. Provided my results are valid, otters stay closer to the ocean than mink. If so, otters will have minimal effect on mink occupying the innermost areas of a watercourse, this would especially benefit the mink during the first stages of colonization or recolonization of areas where adaptive management are conducted.

Generally, riparian landscapes and watercourses in Scandinavia have heterogeneous vegetation zones and patches alongside the rivers, thus making biodiversity high in such areas (Gundersen et al., 2010; Naiman et al., 2005). Even at low fish densities, the abundance of terrestrial prey will probably be sufficient to support a viable mink population in most riparian habitats.

This study could not find a significant relationship between mink presence and salmonid density, but the data points in the direction of a positive relationship. More sites have to be fished to get a clear picture of the actual density of salmonids across the watercourse.

A question that has been raised during this study is the relationship between mink and pine marten. Recommendations for further research are to investigate the elusive relationship between mink and pine marten and to find out if these two mustelids of almost the same size display some sort of competition. Further, it would be of interest to investigate the diet of the mink and perhaps compare it to the diet of the otter and pine marten to determine niche overlap and possibly niche partitioning.

6. References

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Appendix A

Table A1. A list over species that were divided into functional groups before the statistical analysis. There were 194 observations of passerines, 10 observations of ground nesters, and 15 observations of Anseriformes. The group small mustelids were only used in the ordination. n = the number of sites with observations of the respective species.

Group	Scientific name	Common name	n
Passerines	*Acanthis flammea*	Common redpoll	1
	Anthus pratensis	Meadow pipit	1
	Chloris chloris	European greenfinch	1
	Cyanistes caeruleus	Eurasian blue tit	5
	Emberiza citrinella	Yellowhammer	2
	Erithacus rubecula	European robin	25
	Ficedula hypoleuca	European pied flycatcher	1
	Fringilla coelebs	Common chaffinch	16
	Fringilla montifringilla	Brambling	5
	Motacilla alba	White wagtail	2
	Motacilla cinerea	Grey wagtail	1
	Parus major	Great tit	12
	Passer montanus	Eurasian tree sparrow	1
	Phylloscopus trochilus	Willow warbler	4
	Prunella modularis	Dunnock	2
	Pyrrhula pyrrhula	Eurasian bullfinch	1
	Regulus regulus	Goldcrest	1
	Spinus spinus	Eurasian siskin	1
	Sylvia atricapilla	Eurasian blackcap	1
	Sylvia borin	Garden warbler	1
	Troglodytes troglodytes	Eurasian wren	7
	Turdus sp.	Thrush	17
	Turdus iliacus	Redwing	28
	Turdus merula	Blackbird	27
	Turdus philomelos	Song thrush	15
	Turdus pilaris	Fieldfare	16
Ground nesters	*Actitis hypoleucos*	Common sandpiper	6
	Scolopax rusticola	Eurasian woodcock	1
	Tetrao urogallus	Capercaillie	1
	Tetrastes bonasia	hazel grouse	2
Anseriformes	*Anas crecca*	Eurasian teal	5
	Anas platyrhynchos	Mallard	6
	Cygnus cygnus	Whooper swan	1
	Mergus merganser	Common merganser	3
Small mustelids	*Mustela erminea*	Stoat	3
(only for ordination)	*Mustela nivalis*	Least weasel	5

Table A2. List of explanatory variables used in the logistic regression analysis. n = the number of sites with observations of the respective species or group. See table A1 for information on the prey species.

Groups		Scientific name	Common name	n
Competitors/Predators		*Lutra lutra*	Eurasian otter	45
		Martes martes	Pine marten	34
		Meles meles	Badger	21
		Mustela erminea	Stoat	3
		Mustela nivalis	Least weasel	5
		Vulpes vulpes	Red fox	31
Prey	(see table A1)	Anseriformes	-	12
	(see table A1)	-	Ground nesters	10
		Lepus timidus	Mountain hare	4
	(see table A1)	*Passeriformes*	Passerines	86
		Rodentia	Rodents	47
Other sympatric species		*Alces alces*	Moose	20
		Ardea cinerea	Heron	10
		Capreolus capreolus	Roe deer	46
		Sciurus vulgaris	Red squirrel	9

Table A3. List of all terrestrial and aquatic habitat variables measured in field or by GIS.

Habitat	Variable	Abbr.	Data type I	Data type II	Unit
Terrestrial	Bank type	BaTy	Categorical	Nominal	
	Bank height	BaHe	Numerical	Continuous	cm
	Bank substrate		Categorical	Nominal	
	Ferns/Horsetail	Fe/Ho	Categorical	Nominal	
	Graminoids	Gr	Categorical	Nominal	
	Herbaceous		Categorical	Nominal	
	Field shrub	FS	Categorical	Nominal	
	Bryophyte/Lichens		Categorical	Nominal	
	Juniper		Categorical	Nominal	
	Salix sp./multi stem	*Salix* sp.	Categorical	Nominal	
	Rubus sp.		Categorical	Nominal	
	Pine		Categorical	Nominal	
	Spruce		Categorical	Nominal	
	Deciduous		Categorical	Nominal	
	Habitat complexity		Categorical	Ordinal	
	Stems per 5 m		Numerical	Discrete	
	Relascope		Numerical	Discrete	
	Canopy openness	CaOp	Numerical	Continuous	%
	Deadwood on land	DWL	Categorical	Nominal	
	Land use		Categorical	Nominal	
	Distance to main river	DiRi	Numerical	Continuous	m
	Distance to the ocean	DiOc	Numerical	Continuous	m
Aquatic	River ID		Categorical	Nominal	
	Land-water angel	LWA	Numerical	Continuous	degrees
	Deadwood in river	DWR	Categorical	Nominal	
	Average river width	WiAv	Numerical	Continuous	m
	Average river depth	DeAv	Numerical	Continuous	cm
	Distance between extremes	DBE	Numerical	Continuous	m
	Surface velocity	Vel	Numerical	Continuous	m/s
	Bottom substrate		Categorical	Nominal	
	Aquatic vegetation	AqVe	Categorical	Nominal	

* Abbr. = abbreviation.

Appendix B
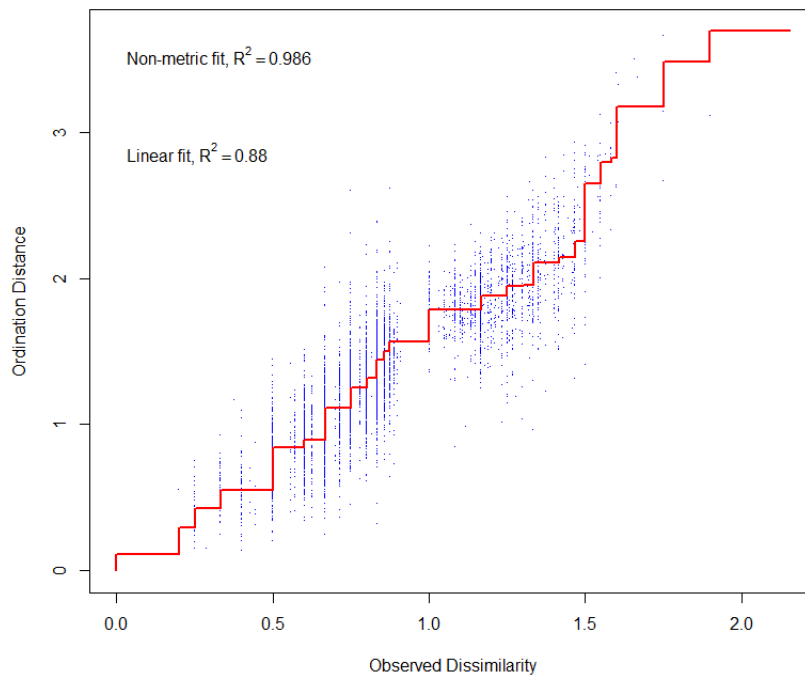
Figure B1. The Shepard stress plot illustrates how the NMDS configuration in four dimensions matches the original data patterns; the fit between the data dissimilarity and the ordination distances is indicated by the monotonic red step line. The non-metric fit is based on stress S and defined as R2 = 1-S*S. The squared correlation between fitted values and ordination distances is represented as 'linear fit'. The non-metric fit value of 0.986 indicates a good fit.
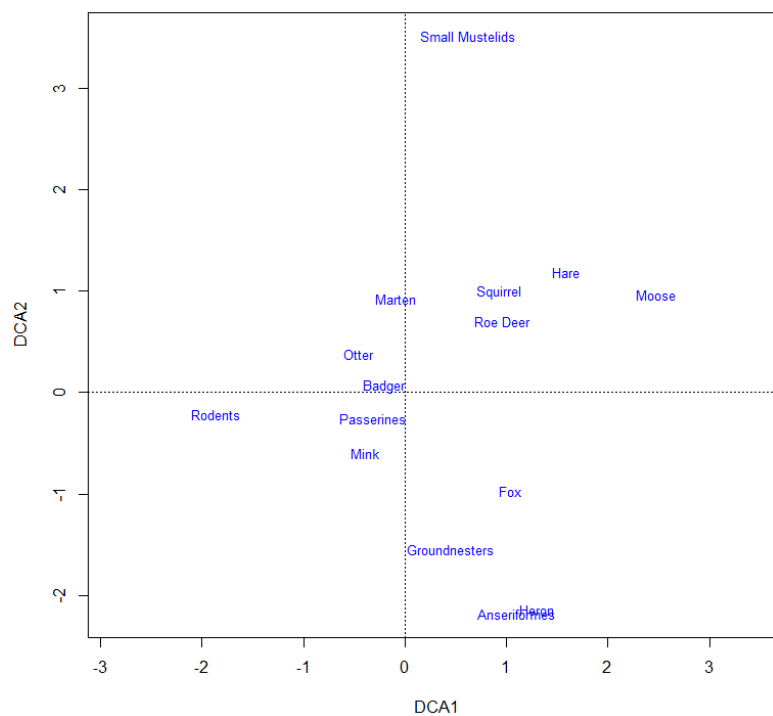
Figure B2. The DCA plot visualize the species community structure. Here we see that mink is closely associated with passerines but further away from ground nesters and pine marten than in the NMDS plot. Down weighting of rare species was applied to the DCA.

Appendix C

Table C1. Model selection table showing the competition models within a range of ΔAICc 0 – 2. The outlined model (no 3) was chosen as the 'best-fit' competition model (residual deviance: 145.32 on 139 df) and the variable *Martes martes* was retained for the second step of the analysis. K = the number of parameters in the respective candidate model.

Model	*L. lutra*	*M. martes*	*M. erminea*	K	ΔAICc	w_i
1		✓	✓	3	0.00	0.311
2	✓	✓	✓	4	0.45	0.249
3		✓		2	0.48	0.245
4	✓	✓		3	0.93	0.195
Null				1	4.13	0.013

Table C2. Model selection table showing prey models within ΔAICc < 2. The outlined model (no 2) was chosen as the most parsimonious model and 'passerines' were retained for the second step of the analysis (residual deviance: 140.53 on 139 df). Gro. nesters = Ground nesters.

| Model	Anseriformes	Gro. nesters	*L. timidus*	Passerines	K	ΔAICc	w_i
1	✓			✓	3	0.00	0.322
2				✓	2	0.70	0.228
3		✓		✓	3	1.46	0.155
4	✓	✓		✓	4	1.47	0.155
5	✓		✓	✓	4	1.66	0.141
Null					1	9.13	0.002

Table C3. Model selection table showing sympatric species (that is not linked to either competition, predation, or prey) models within ΔAICc < 2. The null model was ranked first, so therefore none of the other sympatric species were retained for the second step of the analysis.

Model	*A. alces*	*A. cinera*	*C. capreolus*	*S. vulgaris*	K	ΔAICc	w_i
Null					1	0.00	0.238
1		✓			2	0.43	0.191
2				✓	2	1.21	0.130
3	✓				2	1.21	0.130
4	✓	✓			3	1.54	0.110
5			✓		2	1.62	0.106
6		✓		✓	3	1.83	0.095

Table C4. Model selection table showing candidate models with terrestrial habitat variables within ΔAICc < 2 and the null model. Model nr. 12 were chosen based on the least number of parameters (residual deviance: 133.62 on 137 df). Bank height, *Salix* sp., and Spruce were retained for the second step of the analysis. Notice that all three habitat variables are included in all candidate models.

Model	BaHe	BaTy	CaOp	DWL	Fe/Ho	FS	Gr	*Rubus*	*Salix*	Spruce	K	ΔAICc	w$_i$
1	✓				✓			✓	✓	✓	6	0.00	0.054
2	✓				✓				✓	✓	5	0.18	0.049
3	✓	✓			✓			✓	✓	✓	7	0.19	0.049
4	✓	✓			✓		✓		✓	✓	7	0.34	0.046
5	✓	✓			✓		✓	✓	✓	✓	8	0.35	0.045
6	✓	✓			✓				✓	✓	6	0.37	0.045
7	✓							✓	✓	✓	5	0.61	0.040
8	✓				✓		✓	✓	✓	✓	7	0.92	0.034
9	✓				✓		✓		✓	✓	6	0.92	0.034
10	✓	✓		✓	✓			✓	✓	✓	8	1.04	0.032
11	✓	✓						✓	✓	✓	6	1.13	0.031
12	✓								✓	✓	4	1.18	0.030
13	✓		✓		✓			✓	✓	✓	7	1.29	0.028
14	✓	✓	✓		✓				✓	✓	7	1.31	0.028
15	✓	✓	✓		✓		✓	✓	✓	✓	9	1.39	0.027
16	✓				✓	✓		✓	✓	✓	7	1.42	0.027
17	✓	✓	✓		✓		✓		✓	✓	8	1.45	0.026
18	✓		✓		✓				✓	✓	6	1.48	0.026
19	✓	✓			✓	✓		✓	✓	✓	8	1.48	0.026
20	✓					✓		✓	✓	✓	6	1.54	0.025
21	✓				✓	✓			✓	✓	6	1.58	0.025
22	✓	✓					✓	✓	✓	✓	7	1.58	0.025
23	✓						✓	✓	✓	✓	6	1.62	0.024
24	✓	✓	✓		✓		✓		✓	✓	8	1.66	0.024
25	✓	✓							✓	✓	5	1.67	0.024
26	✓		✓		✓				✓	✓	6	1.70	0.023

Model	BaHe	BaTy	CaOp	DWL	Fe/Ho	FS	Gr	*Rubus*	*Salix*	Spruce	K	ΔAICc	w$_i$
27	✓	✓			✓	✓	✓	✓	✓	✓	9	1.70	0.023
28	✓	✓			✓	✓			✓	✓	7	1.72	0.023
29	✓	✓			✓	✓	✓		✓	✓	8	1.78	0.022
30	✓	✓					✓		✓	✓	6	1.82	0.022
31	✓		✓		✓			✓	✓	✓	7	1.86	0.021
32	✓	✓					✓	✓	✓	✓	7	1.90	0.021
33	✓						✓		✓	✓	5	1.92	0.021
Null											1	12.32	0.000

Abbreviations: BaHe = Bank height, BaTy = Bank type, CaOp = Canopy openness, DWL = Deadwood on land, Fe/Ho = Ferns/Horsetail, FS = Field shrub, Gr = Graminoids, *Rubus* = *Rubus* sp., *Salix* = *Salix* sp.

Table C5. Model selection table showing candidate models with aquatic habitat variables within ΔAICc < 2. The null (intercept) model is among the set of candidate models (marked in blue), therefore, aquatic habitat models were discarded and not used in the second part of the analysis.

Model	AqVe	DeAv	DBE	DiOc	DiRi	River	Vel	WiAv	K	ΔAICc	wi
1							✓		2	0.00	0.141
Null									1	0.59	0.105
2	✓						✓		4	0.73	0.098
3	✓		✓				✓		5	1.46	0.068
4			✓				✓		3	1.48	0.067
5							✓	✓	3	1.54	0.066
6	✓								3	1.59	0.064
7						✓	✓		5	1.62	0.063
8					✓		✓		3	1.85	0.056
9						✓			4	1.86	0.056
10		✓							2	1.88	0.055
11				✓			✓		3	1.90	0.055
12		✓					✓		3	1.95	0.053
13	✓		✓						4	1.98	0.053

Abbreviations: AqVe = Aquatic vegetation, DeAv = Average depth, DBE = Distance between extremes, DiOc = Distance to the ocean, DiRi = Distance to the main river, Vel = (water) Velocity, WiAv = Average width.

Table C6. Model selection table displaying the two candidate models within ΔAICc < 2 and the null model derived from the final model. The 'winner' model (no. 1) is marked in blue and contain bank height, passerines, and spruce as explanatory variables (residual deviance: 128.52 on 137 df).

Models	Bank height	*M. martes*	Passerines	Spruce	K	ΔAICc	wi
1	✓		✓	✓	4	0.00	0.52
2	✓	✓	✓	✓	5	0.19	0.47
Null					1	16.25	0

Table C7. Model selection table showing the only candidate model from the fish model under ΔAICc 2. The model only contained 'density of trout per 100 m^2' (residual deviance: 23.961 on 34 df).

Model	Trout 100 m^2	K	ΔAICc	wi
1	✓	2	0.00	1
Null		1	2.81	0

Table C8. Model selection table showing the two candidate models within ΔAICc < 2 from the otter and proximity to the ocean or the main river model. Model nr 1 containing only 'distance to the ocean' as explanatory variable was chosen based on least parameters (residual deviance: 167.46 on 139 df).

Model	Dist. Ocean	Dist. River	K	ΔAICc	w_i
1	✓		2	0.00	0.72
2	✓	✓	3	1.99	0.26
Null			1	7.08	0.02

Appendix D

MINK MODEL RESULTS:

Observations: 141

Dependent Variable: Neovison vison

Type: Generalized linear model

  Family: binomial

  Link function: logit

MODEL FIT:

Null deviance: 151.03 on 140 df

Residual deviance: 128.52 on 137 df

Pseudo-R² (McFadden) = 0.15

Standard errors: Maximum Likelihood Estimation

AICc = 136.52

Table D1. The output from the final model. The estimates show that presence of passerines and spruce have a positive effect on the likelihood of mink detection. Bank height has the opposite effect, increased bank height decreases the likelihood of detecting mink.

	Estimate	S.E.	Z val.	p
(Intercept)	-1.93	0.65	-2.96	0.00
Passerines (presence)	1.46	0.54	2.70	0.01
Bank height	-0.02	0.01	-2.69	0.01
Spruce (presence)	1.16	0.51	2.27	0.02

FISH MODEL RESULTS:

Observations: 36

Dependent Variable: Neovison vison

Type: Generalized linear model

  Family: binomial

  Link function: logit

MODEL FIT:

Null deviance: 29.012 on 35 df

Residual deviance: 23.961 on 34 df

Pseudo-R² (McFadden) = 0.17

Standard errors: Maximum Likelihood Estimation

AICc = 27.96

Table D2. The output from the final fish model. The estimates indicate a positive relationship between the density of trout per 100 m^2 and the likelihood of detecting mink, though it was not significant.

	Estimate	S.E.	Z val.	p
(Intercept)	-3.09	0.92	-3.36	<0.001
Trout 100m^2	0.04	0.02	1.78	0.08

OTTER MODEL RESULTS:

Observations: 141

Dependent Variable: Lutra lutra

Type: Generalized linear model

  Family: binomial

  Link function: logit

MODEL FIT:

Null deviance: 176.60 on 140 df

Residual deviance: 167.46 on 139 df

Pseudo-R² (McFadden) = 0.05

Standard errors: Maximum Likelihood Estimation

AICc = 171.46

Table D3. Output from the final otter model. The parameter 'distance from the ocean' showed a negative relationship to the detection rate of otters.

	Estimate	S.E.	Z val.	p
(Intercept)	0.37	0.41	0.89	0.37
Dist. to ocean (km)	-0.10	0.03	-2.92	<0.001