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**Master Thesis**

**Influence of vole cycles and other  
environmental factors on pine marten  
(*Martes martes*) population dynamics and  
abundance in southeastern Norway**

**Master in Applied Ecology**

**2022**

## **Acknowledgements**

I wish to thank my supervisors, Morten Odden, Scott Michael Brainerd, Torfinn Jahren for their comments and guidance. A special thanks to Olivier Devineau for helping me with the statistics. I am grateful for the thorough and valuable feedback I got from Kjartan Østbye. I want to thank Ana Peris for telling me to not give up, her useful comments, input and support. My parents, for their support. My two brothers, Henrik and Sigurd, for the recreational value and joy you provided.

## Abstract

The pine marten in Norway lives at the northern edge of their distribution area. At this latitude, regular fluctuations in vole population sizes are common, where the amplitudes get more pronounced with increasing latitude. This dynamic plays an important role in the ecosystem, as voles are prey for many predators, being a major part of the diet for the pine marten. However, the temporal and causal relationship between pine marten and vole fluctuations has received little attention, particularly regarding how vole peaks and lows affect pine marten population dynamics. Using snow tracking indices from previously sampled 618 yearly line transects covering eleven years in Hedmark county, Southeastern-Norway, I estimated the pine marten abundance, and investigated how pine marten abundance responded to vole fluctuations. I studied how these potential co-dynamics behaved in a north-south gradient, including the parameters snow depth and vole abundance (from prior data collections) upon the response variable pine marten abundance from snow tracks (i.e., tracks per km<sup>2</sup>). Pine marten abundance was expressed as binomial in order to reduce noise, and binomial regression models were used with snow depth, vole abundance and human settlement density. In order to test for cyclicity, snow track indices were used in Partial Rate Correlation Function, and the combined residuals was used as a response variable with snow depth, elevation and vole coefficient of variation.

I predicted that pine martens were synchronized with vole fluctuations, and that the cyclicity was more pronounced in the northern part of the study area. The results showed that pine marten population size was positively associated with the previous year's vole abundance and snow depth. A possible explanation can be the pine marten physiology, and adaptation to snow. The pine marten abundance was negatively associated with human settlement density, indicating vulnerability towards anthropogenic impacts. Pine marten population dynamics displayed a strong density-dependent growth pattern and showed no signs of cyclicity. The growth pattern was negatively affected by variation in vole abundance and increased elevation, while positively associated with snow depth, indicating that the population dynamics differs on a north-south gradient. The prediction that the pine marten is cyclic was not supported, albeit it is clear that voles are a vital part of the pine marten diet, it's life history traits might explain why it is not synchronized with vole fluctuations. Possible explanations here include food caching, shifting to alternative prey and intraspecific regulation mitigating effects of varying access to voles as prey.

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# Contents

<b>1.</b>	<b>INTRODUCTION .....</b>	<b>5</b>
<b>2.</b>	<b>MATERIAL AND METHODS .....</b>	<b>9</b>
2.1	STUDY AREA .....	9
2.2	DATA COLLECTION .....	11
2.2.1	<i>Pine marten snow track data.....</i>	<i>11</i>
2.2.2	<i>Data collection for voles .....</i>	<i>12</i>
2.2.3	<i>Habitat data collection.....</i>	<i>13</i>
2.3	STATISTICAL ANALYSES .....	13
<b>3.</b>	<b>RESULTS.....</b>	<b>15</b>
3.1.1	<i>Pine marten abundance.....</i>	<i>15</i>
3.1.2	<i>Partial rate correlation function .....</i>	<i>17</i>
3.1.3	<i>Pine marten density dependence .....</i>	<i>18</i>
<b>4.</b>	<b>DISCUSSION.....</b>	<b>20</b>
4.1	DENSITY DEPENDENCE, ELEVATION, VOLE ABUNDANCE AND FLUCTUATIONS .....	21
4.2	SNOW DEPTH & SETTLEMENT DENSITY.....	23
<b>5.</b>	<b>REFERENCES .....</b>	<b>26</b>

# 1. Introduction

The study of population dynamics as a fundamental ecological concept attempts to explain how populations of living organisms stabilize, increase and decrease in numbers (Berryman, 1999; Hastings, 2013), and what factors influence this change. No population can grow infinitely, and how factors regulate or limit the growth of a population, is often dependent on its density. Density dependent factors occur when a population reaches a certain number, and can be predation, competition over resources, or diseases. These factors can have either a negative or a positive relationship with population growth, and density independent factors are typically abiotic, and it affects a population regardless of their density. Example of density independent factors is e.g. snow, which can be a limiting factor for red fox (*Vulpes vulpes*) (Bartoń & Zalewski, 2007), or low temperatures, which was a limiting factor for the population growth of the European golden plover (*Pluvialis apricaria*) during severe winters (Yalden & Pearce-Higgins, 1997). Anthropogenic activity can be either limiting or regulating, and it has been well documented that disturbances caused by human development can have adverse effect on species abundance and composition (Johnson & St-Laurent, 2011). Population dynamics may also change with latitude, and in Europe, this is apparent in small rodent populations, who displays cyclic fluctuations in abundance at higher latitude and altitude (Andreassen et al., 2019; Krebs, 2013).

Many species undergo regular cyclic population fluctuations such as the grey larch budmoth (*Zeiraphera diniana*) who reproduces in large quantities every 8-10 years in the European alps (Berryman & Turchin, 2001; Wermelinger et al., 2018), and the snowshoe hare whose 10-year cycles occur in synchrony across North-America (Krebs et al., 2001). In Europe, voles and lemmings (*Arvicolinae*), are cyclic with a 3-5 year interval, and have been extensively studied for a century (Elton, 1924; Kleef & Wijsman, 2015; Korpimäki et al., 1991; Krebs, 2013). Vole abundance can vary dramatically between population peaks and lows (Andreassen et al., 2021). The underlying mechanisms and drivers behind these cycles are still not fully understood, even after decades of research, and several hypotheses have been proposed to explain the phenomenon. Two examples are the mast depression theory, which suggest that vole fluctuations in turn are a result of cyclic seed cropping (Selås, 1997), and the predation hypothesis which suggests that small mustelids are the driving force behind the population cycles (Andersson & Erlinge, 1977; Korpimäki et al., 1991; Korpimäki & Krebs, 1996). In

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Europe, population outbreaks occur when rodents (*Rodentia*) multiply in numbers over a short period of time (Jacob et al., 2020; Singleton et al., 2010). These outbreaks become more regular with increasing latitude and altitude, and above 60°N, multiannual fluctuations in population sizes are common (Singleton et al., 2010). The amplitudes of the cycles are positively associated with increasing latitude (Krebs, 2013). These cycles are not limited to Northern Europe. Examples of vole cycles have been found in Central Europe in Poland and Czech Republic (Tkadlec & Stenseth, 2001), but population cycles here do not display the same strong amplitudes as in Fennoscandia. In Norway, these cycles are apparent in bank voles (*Myodius glareolus*), field voles (*Microtus agrestis*) and lemmings (*Lemmus lemmus*), and these cycles can be synchronous over large areas (Ims & Andreassen, 2000). Microtine voles are a key species in many ecosystems, and function as prey for both terrestrial and avian predators as well as contributing to nutrient recycling and seed dispersal (Ecke et al., 2017). Their population fluctuations can strongly influence the population dynamics of predators (Weber et al., 2002). There is a positive association between vole abundance and small predator abundance, such as stoat (*Mustela erminea*) and least weasels (*Mustela nivalis*) and pine marten (Cano-Martínez et al., 2021). Stoats and weasels are considered vole specialists, and are strongly affected by the vole cycles (Korpimäki et al., 1991). As for the red fox, which is a generalist, is also affected by the vole cycles (Lanszki et al., 2007). As for the pine marten, microtines are an important part of their diet (Helldin, 2000; Helldin, 1999; Jędrzejewski et al., 1993; Pulliainen & Ollinmaki, 1996), but the relationship between pine martens and vole cycles have received little attention.

The European pine marten belongs to the family *Mustelidae*, and has a wide distribution range across Eurasia, from Portugal to Russia (Ruiz-González et al., 2013). Pine martens is similar to a house cat (*Felis catus*) in size, with males being larger than females (Baumann & Gornetzki, 2017). They have an elongated body shape, with poor insulative properties due to short fur and the high surface to volume ratio (Worthen & Kilgore, 1981). Pine marten reproductive biology is characterized by delayed implantation (Ferguson & Larivière, 2005). This is a life history trait common to many mammals (Ptak et al., 2012), meaning that while breeding occurs during summer, blastocysts do not implant until the following winter to ensure that the kits are born during spring. This is to ensure that the kits have a higher chance of postnatal survival (Fenelon & Renfree, 2018). Considered a habitat specialist, pine martens prefer forested habitats, ranging from deciduous forests in the south, to coniferous pine forests in the north, however they may

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also inhabit shrublands and fragmented wooded areas (Brainerd & Rolstad, 2002; Lombardini et al., 2015). In southern boreal Scandinavia, they avoid open areas such as bogs, clear cuts and fields (Brainerd & Rolstad, 2002), where they might be exposed to potential predators such as the red fox (Lindström et al., 1995) or raptor species such as the golden eagle (*Aquila chrysaetos*) (Sulkava et al., 1999). In Scandinavia, pine martens are typically found in mature, spruce-dominated forests (Brainerd & Rolstad, 2002). Resting sites are found in rocky substrates or in abandoned squirrel nests in spruce trees (*Picea abies*), and natal dens are typically located in cavities of either Scots pine (*Pinus sylvestris*) or Aspen (*Populus tremula*) (Brainerd et al., 1995). Pine martens are solitary animals that defend territories which vary in size from 2 to 25 km<sup>2</sup>, depending on habitat quality, food access, gender, and habitat fragmentation (Brainerd, 1997; Zalewski & Jedrzejewski, 2006). Males also tend to occupy larger territories than females (Zalewski & Jedrzejewski, 2006), and the social structure is characterized by intra-sexual exclusion and intersexual overlap (O'Mahony, 2014). The pine marten is an opportunistic generalist whose diet can vary seasonally, and consists of small rodents such as squirrels and voles, hares, ungulate carcasses and other carrion, passerines and their eggs, insects, mushrooms, and berries. It caches these food items in order to prepare for scarcer abundance of prey in wintertime (Helldin, 2000; Twining et al., 2018).

Numerical responses in mustelids in relation to vole cycles have been a subject of interest for many decades (Hanski et al., 1991), and both least weasels and stoats are synchronized with fluctuations in vole abundance (Korpimäki et al., 1991; Turchin & Hanski, 1997). Studies from southern Sweden showed that pine marten population in the southern boreal regions were not affected significantly by vole cycles, and did not show a strong numerical response to low vole abundances (Helldin & Lindström, 1995; Helldin, 1999). However, the authors indicate that this was probably due to the lower amplitude in vole cycles during the study, and that the absence of the amplitudes lasted for a decade (Hörnfeldt, 2004). With a more typical vole fluctuation regime in Scandinavia, one might observe more pronounced numerical responses. Others postulate that the functional response of pine martens by switching to different prey might mitigate this effect (Jędrzejewski et al., 1993; Pulliainen & Ollinmaki, 1996; Zalewski et al., 1995). A study from Białowieża forest in Poland, indicated a positive relationship between vole- and pine marten abundance, and that pine martens had a functional response to low vole numbers, and switched over to other prey (Zalewski, 2007; Zalewski & Jedrzejewski, 2006).

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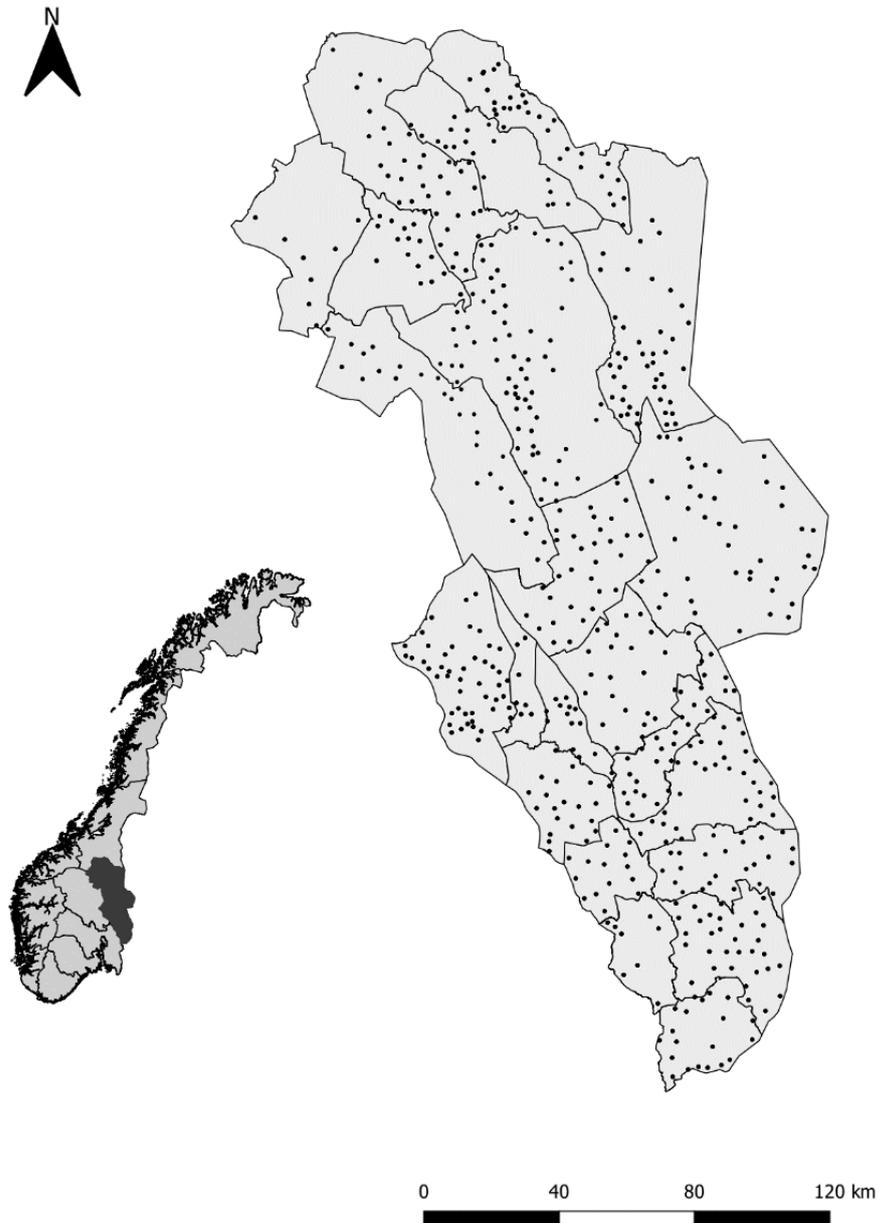
The aim of this study was to investigate the relationship between pine marten and vole population dynamics. I used spatiotemporal data spanning eleven years across a varying gradient of climate, landscape productivity and anthropogenic impact. This gave me an opportunity to investigate how fluctuating prey together with biotic and abiotic factors influenced pine marten dynamics and abundance. The objectives of this study were to 1) determine if voles were a primary driver of pine marten population dynamics, and 2) to what extent this predator-prey relationship was modulated by important environmental factors (snow depth, elevation, settlement density and rodent abundance and variation of abundance) at a regional scale. My predictions were that pine marten population size is synchronized with vole peaks and lows, and are following vole fluctuations, and that the cyclicity is more pronounced in the northern part of the study area, than in the south of Hedmark county.

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## 2. Material and methods

### 2.1 Study area

This study was conducted in former Hedmark county (27, 400km<sup>2</sup> where 13, 000 km<sup>2</sup> is forest.), which is a part of Inland County today (Figure 1). During the study period 2003-2014, Hedmark county had a mean human population of 190 402, with a mean density of 6.9 people per square kilometer (*Statistics Norway*, n.d.). The county stretches from lush areas in the south, dominated by agricultural landscape and with mild winters, to mountainous areas in the north, with the agricultural areas limited to river valleys (Moen, 1999; Figure 2). Hedmark county stretches from 59°N to 62°N, and the difference in elevation ranges from 123 meters above sea level, to 2 178 (Figure 2) meters. Roughly half of Hedmark is forested, in a landscape fragmented by clearcuts, agriculture and infrastructure. Forests are comprised primarily of Scot's pine, and Norway spruce, interspersed with deciduous trees including white birch (*Betula pubescens*) and aspen. A report from Norwegian Institute of Nature research gives Norwegian forests a low score on the Nature Index (0.41) which ranges from 0 to 1, which is documenting overall status for ecosystems in Norway. A 0 means a degraded ecosystem and a 1 indicates a intact ecosystem (Nybø et al., 2012). The score is relatively low due to logging activities in combination with removal of dead trees and old forest stands (Nybø et al., 2012). In addition, a low number of top-predators in combination with a surging logging industry has led to a high number of moose (*Alces alces*) and other cervids which in turn leads to overgrazing, which negatively affects the biodiversity index (Nybø et al., 2012). The most important industry in Hedmark is logging, mainly of Norway spruce and the dominating method is clear-cuttings (Gustafsson et al., 2010). In these forests, there are three species of cervids: moose, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). All the large predators, Eurasian brown bears (*Ursus arctos*), wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*) and wolverines (*Gulo gulo*), occur in Hedmark county, in addition to mesopredators such as the red fox, European badger (*Meles meles*), and pine martens, and smaller mustelids, stoat and least weasel.



*Figure 1 Map over the study area; Hedmark County with municipal borders in Norway with dots illustrating the center of the 618 transect lines (3 km). Map data retrieved from Norwegian Mapping Authority and created in QGIS.*

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## 2.2 Data collection

### 2.2.1 Pine marten snow track data

Accounts of pine marten tracks were collected along transects each winter. The transects were surveyed in January or February each year between 2003 and 2014 by Hedmark Chapter of the Norwegian Association for Hunters and Anglers (Tovmo & Brøseth, 2014). The pine marten data is comprised of 618 unique transect lines averaging 2.95 km in length (Figure 1). The average density of the transect lines were 3.8/100km<sup>2</sup> of the total area of Hedmark. The mean annual number of transects surveyed was 404, ranging between 281 and 484. Pine marten track data is expressed as binary data for the linear regression models, and as counts for the population dynamics models. These transects were originally established to monitor lynx abundance and reproduction in forested areas (Linnell et al., 2007). Additional variables such as snow depth and days since last snowfall, ranging from 1 to 14 days, were registered, and used for the Partial Rate Correlation Function (PRCF). A total of 4848 pine marten tracks were registered in the 11-year period of the project and are included in this data set.

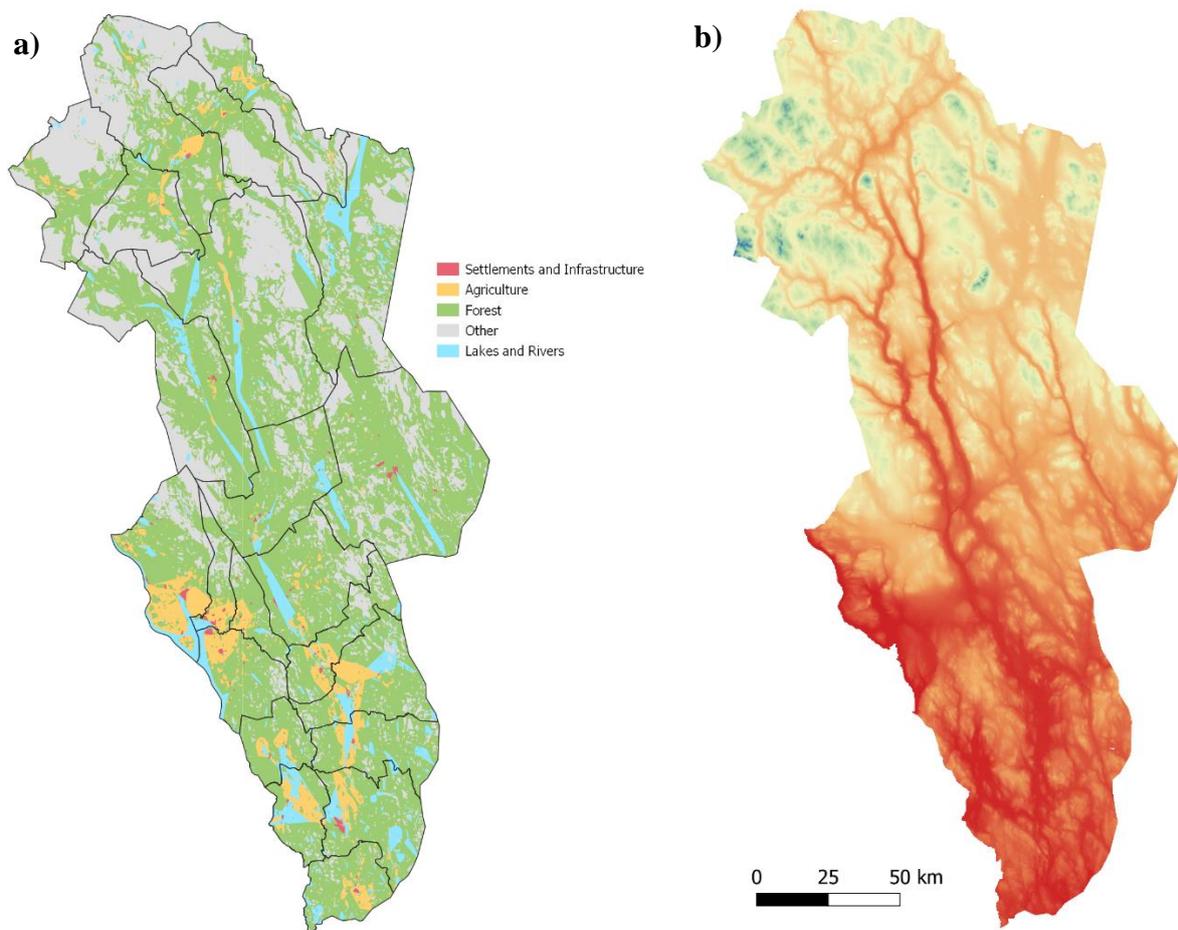


Figure 2 a) Area resource map of Hedmark and b) Digital Elevation Map where the color indicates the elevation. Red (100m+), orange (500+), yellow (1000+) green (1400+), blue (1800+).

## 2.2.2 Data collection for voles

The presence of vole cyclicity in the study area during the time of my study has already been tested and confirmed in another paper (Cano-Martínez et al., 2021), utilizing the same dataset. Although the main dataset includes vole tracks, one has to take into account that voles primarily spend their time in the subnivean space in the winter time (Korslund, 2006), and thus there is an uncertainty about whether or not the vole tracks will work as a reliable indicator of vole cycles. Therefore, I used a time series of vole data collected during management surveys for grouse during August throughout the county (Breisjøberget et al., 2018). The rodent abundance was expressed as presence/absence in the assessment areas where the data was collected. I used Inverse Distance Weighting (IDW) in QGIS (QGIS Development Team, 2021) to create a raster heatmap with values ranging between 0 to 1, where values approaching 0 represent an almost

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absence of voles, and values close to 1 indicates a relatively high abundance of voles. I used the Point Sampling tool with the original coordinates of transect centroids from the pine marten dataset, to retrieve the rodent values from the raster heatmap. To obtain annual vole observations, I used the filter function, and sampled for each raster map in QGIS. In addition to rodent abundance, I calculated the coefficient of variation (CV) for the vole time series in each pine marten transect centroid, to examine the extent of variation in relation to the mean of the population from year to year. The coefficient of variation is a standardized measure of the spread in data points and is calculated as  $SD/mean$  and is used in the PRCF models.

### 2.2.3 Habitat data collection

The variables settlement density and elevation was retrieved from the Norwegian Mapping Authority's N250 Area Usage maps and Digital Elevation Maps (*Norwegian Mapping Authority, 2021*). I used the Kernel Density function in QGIS to create a heatmap of settlement density. I used the Point Sampling tool to extrapolate the settlement density and elevation to the existing transect coordinates. The points used for settlement density ranged from single houses/cabins to small cities, with a higher density of buildings in the south.

## 2.3 Statistical Analyses

I used the lme4 package (Bates et al., 2022) in R to build binomial regression models for pine marten abundance and the effects of habitat using the variable Year as a random factor. Pine marten abundance was expressed as presence/absence, and the explanatory variables were snow depth (cm), rodent abundance, elevation (m), and settlement density. Using presence/absence is in this case, a conservative approach, where the chance of overestimation of individuals is removed. Also, any peaks and lows from year to year, is removed, and I used Pearson's correlation tests in the integrated stats package (R Core Team, 2020) to detect collinearity. There was a strong correlation between elevation and latitude (*Pearson's  $r = 0.84$* ), most likely due to the increasing elevation with latitude in Hedmark county. I retained elevation as the explanatory variable, as it is a function of latitude. Additionally, latitude is negatively correlated with net primary productivity, and plant species richness (Gillman et al., 2014). Thus, the variable elevation is a function of both latitude and productivity. There was also a strong correlation between settlement density and agricultural landscape density, (*Pearson's  $r = 0.87$* )

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and I retained settlement density since it can be an important limiting factor for pine marten abundance, and the relationship between agriculture and pine marten has already been described in another article (Cano-Martínez et al., 2021). A previous study revealed that pine marten densities were positively correlated with abundance of voles the year before (Zalewski & Jedrzejewski, 2006). Thus, I examine the effect of a 1-year lag of voles on pine marten population dynamic, aligning pine marten year with vole year (5 – 6 months after vole data collection), similarly to a previous study with the same data set (Cano-Martínez et al., 2021).

In order to test for potential cyclicity and to identify density dependent structure in the pine marten population, I utilized the Partial Rate Correlation Function (PRCF). The PRCF is an autocorrelation function that is designed to detect density dependent structures in biological populations by correlating the logarithmic per capita rate of change to lagged population densities, using Bartlett's criteria of significance (Berryman & Turchin, 2001). I indexed the marten tracks with the formula:

$$\text{Tracks/Length of transect (3 kilometers)/Days since last snowfall} = X^{*}/3/N$$

The PRCF requires complete (i.e., observations each time-step) time series to converge. Since not all transects were surveyed each year and thus comprise incomplete time series, I grouped, by proximity, transects into 100 transect clusters using the spatstat package in R (Baddeley et al., 2022). The residuals from the PRCF of 100 time series parameterized the response variable in regression models. I then fitted these models with latitude, snow depth, elevation, settlement density, agricultural density, rodent abundance and the coefficient of variance of the vole abundance ( $SD/Mean*100$ ) as the explanatory variables.

Candidate models approximating pine marten abundance and pine marten population dynamics were evaluated using Akaike's information criterion corrected for small sample sizes AICc. For each model set, I included the null model as reference (Table 1, 2).

### 3. Results

#### 3.1.1 Pine marten abundance

The model with the additive effects of *rodent* + *settlement* + *snow* performed better than any other model ( $AICc = 3734$ ,  $\Delta AICc = 0$ ,  $AICcWt = 0.65$ ; Table 1). For the pine marten abundance models, the top three models all included settlement, and when this variable was removed, there was a jump in the  $\Delta AICc$  from 4.18 to 19.11 (Table 1), indicating that settlement is a variable that is important when attempting to explain the variation in track frequency. There was a positive relationship between pine marten abundance and the lagged effect of 1 year of vole abundance  $\pm 2SE$  (Estimate = 0.67, SE = 0.39). Snow depth was also positively associated with pine marten abundance (Estimate = 0.01, SE = 0.01). There was a negative association between pine marten abundance and settlement density (Estimate = -0.37, SE = 0.08) (Figure 3).

*Table 1 Model selection of binomial models with pine marten presence/absence as the response variable, ranked using Aikakes Information Criterion corrected for small sample sizes (AICc). Delta, weight, loglikelihood.*

<i>Model</i>	<i>K</i>	<i>AICc</i>	$\Delta AICc$	<i>AICcWt</i>	<i>Cum.Wt</i>	<i>LL</i>
Rodent + Settlement + Snow	5	3732.31	0	0.65	0.65	-1861.14
Rodent + Settlement + Snow + Elevation	6	3734.07	1.76	0.27	0.92	-1861.02
Settlement : Snow	3	3736.48	4.18	0.08	1	-1865.24
Rodent + Snow	4	3751.42	19.11	0	1	-1871.7
Rodent + Snow + Elevation	5	3751.65	19.35	0	1	-1870.82
Snow	3	3754.01	21.7	0	1	-1874
Rodent + Settlement	4	3754.48	22.17	0	1	-1873.23
Settlement	3	3756.46	24.15	0	1	-1875.22
Rodent : Snow + Elevation	4	3757.57	25.26	0	1	-1874.78
Rodent : Snow	3	3762.52	30.21	0	1	-1878.26
Rodent : Settlement	3	3764.99	32.69	0	1	-1879.49
Rodent + Elevation	4	3776.72	44.41	0	1	-1884.35
Elevation	3	3777.24	44.93	0	1	-1885.62
Rodent + Elevation	3	3782	49.69	0	1	-1888
Rodent	3	3786.16	53.85	0	1	-1890.08
NULL	2	3788.59	56.28	0	1	-1892.29

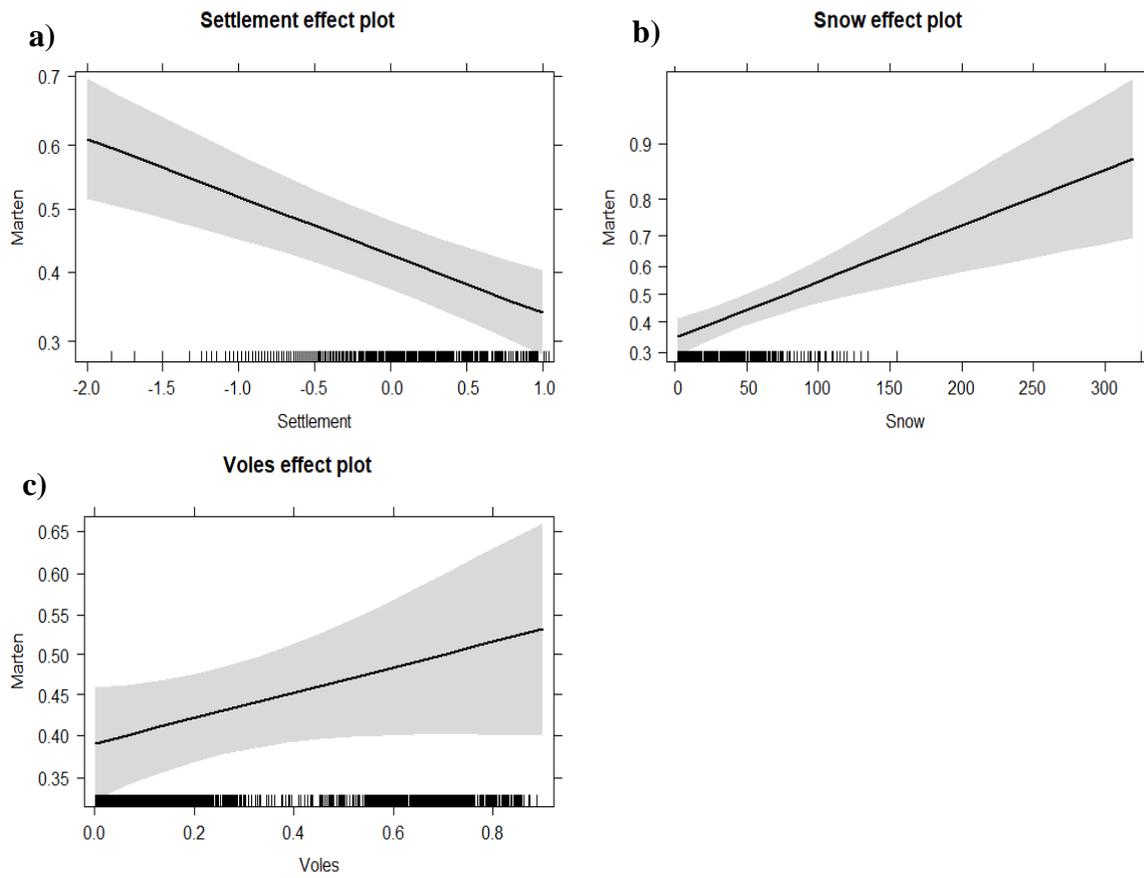
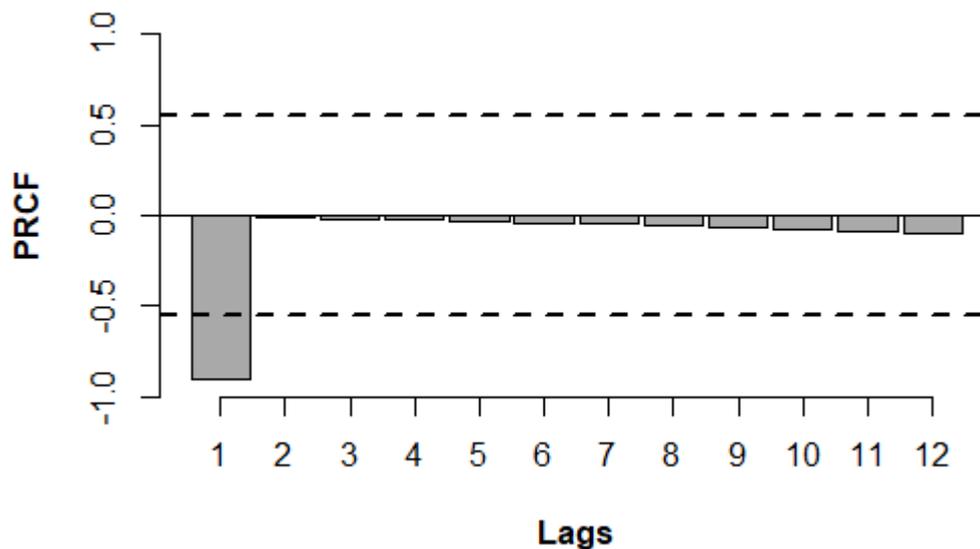


Figure 3 Relationship of settlement density (a), snow depth (b) and vole abundance (c) to pine marten abundance. The black vertical lines on the bottom represents observations of the explanatory variable, the grey shaded area is the confidence interval (CI).

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### 3.1.2 Partial rate correlation function

No cyclic pattern was detected using Bartlett's criteria of significance in any of the time series. The order of feedback-delay shows that direct density dependence was the dominating growth pattern in the pine marten population in Hedmark (Figure 4). The residuals from the PRCF model can be understood as the amount of change in a population. Values close to zero indicated little change. Meaning that when you have a negative relationship between a residual and a variable, it is an indicator of a stabilizing population.



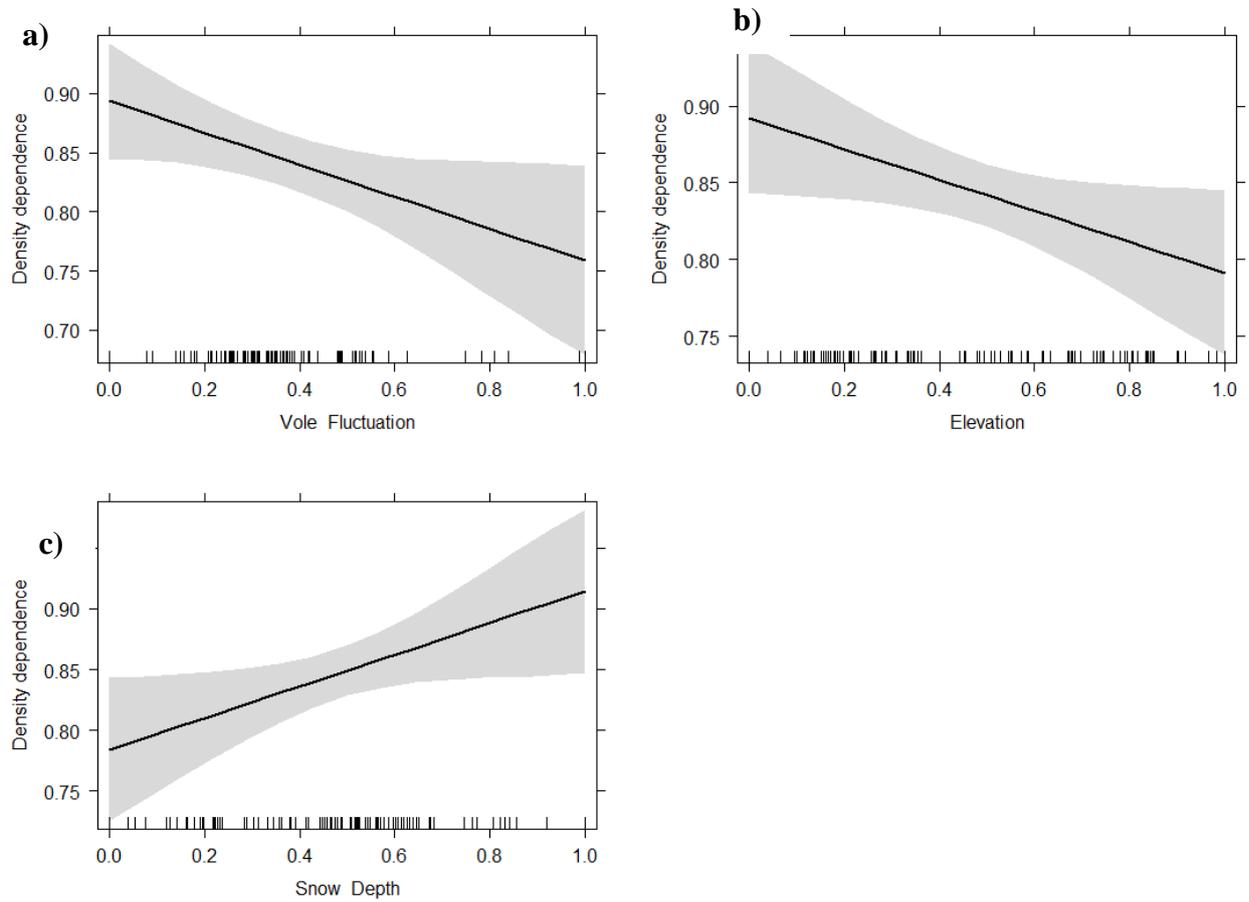
*Figure 4 Example of the partial rate correlation function (PRCF) for pine marten extracted from one of the residual groups. Here to illustrate the direct density dependence, and the lack of cyclicity using Bartlett's criteria of significance, and that lag 1 is the dominating growth structure in the pine marten population. Meaning that the size of the population is dependent on the size the previous year, and thus directly density dependent.*

### 3.1.3 Pine marten density dependence

The model selection for population density dependence models (Table 2) produced two models for further inference, where the model with the additive effects of *rodent variation*+ *elevation* + *snow* (AICc = -164.81,  $\Delta$ AICc = 0; Table 2) was chosen. Elevation (Estimate = -0.10, SE = 0.05; Figure 5), and vole variation (Estimate = -0.14, SE = 0.06; Figure 5) were negatively associated with the marten density dependent growth. Snow depth (Estimate = 0.13, SE = 0.06; Figure 5) was positively associated with the direct density dependent growth.

*Table 2 Model selection of population density dependence models ranked using Aikakes Information Criterion corrected for small sample sizes (AICc). Delta, weight, loglikelihood.*

<i>Model</i>	<i>K</i>	<i>AICc</i>	$\Delta$ <i>AICc</i>	<i>AICcWt</i>	<i>Cum. Wt</i>	<i>LL</i>
Rodent variation + elevation + snow	5	-164.81	0	0.41	0.41	87.73
Rodent variation	3	-163.37	1.44	0.2	0.62	84.81
Rodent variation + elevation	4	-162.29	2.51	0.12	0.73	85.36
Snow depth	3	-160.54	4.26	0.05	0.78	83.40
Rodent variation : elevation	3	-160.20	4.61	0.04	0.82	83.23
Rodent variation : snow	3	-160.10	4.71	0.04	0.86	83.18
Rodent variation : Settlement	3	-159.72	5.09	0.03	0.9	82.99
NULL	2	-159.63	5.18	0.03	0.93	81.88
Settlement density	3	-159.59	5.22	0.03	0.96	82.92
Elevation	3	-157.93	6.88	0.01	0.97	82.09
Rodents	3	-157.80	7.01	0.01	0.98	82.02
Agricultural density	3	-157.51	7.30	0.01	1	81.88
Rodent + elevation	4	-155.90	8.91	0	1	82.16



*Figure 5 Relationship between vole fluctuation (a), elevation (b), snow depth (c) and pine marten density dependence. The vertical black lines on the bottom are the elevation points, the gray shaded area is the confidence interval.*

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## 4. Discussion

My prediction that the pine marten is cyclic, and that the degree of cyclicity varies with latitude, was not supported. My results show that pine marten abundance was positively associated with snow depth and vole abundance with a 1-year time lag, whilst pine marten abundance was negatively associated with settlement density. I did not detect cyclicity in the pine marten population, but the population growth pattern was directly density dependent. Snow depth had a positive relationship with the direct density dependence, whilst vole fluctuations were negatively associated with the degree of density dependence. Elevation, which functions as a proxy for productivity and latitudinal gradient in Hedmark county, were negatively correlated with direct density dependence, thus indicating that the degree of direct density dependence weakens with increasing latitude.

Track counts on snow can be used as a reliable method to infer population abundance and population dynamics (Kawaguchi et al., 2015). It is a non-invasive method with a higher detection rate than camera trapping and track plates, and that have compared track frequencies with population size show that the number of tracks is proportional to the population size (Kawaguchi et al., 2015), and tracks and similar indirect signs can function as a proxy of population density. However, Snow tracking can have several biases such as observer bias and misidentification of tracks. Very low temperatures can lower the activity level of the closely related American marten (*Martes americana*) (Thompson & Colgan, 1994), and lower activity levels has been observed in European pine marten during low temperatures in Poland (Zalewski, 2006), which can result in lower track counts during periods of very cold weather. However, temperature was not recorded during the data collection. The frequency of tracks can also be affected by the number of martens in an area, social activity and interspecific interactions. Additionally, detection probabilities can be influenced by habitat, site-specific conditions, sampling effort and density (Smith et al., 2007). This is partly considered for the linear regression models, where much of the noise, observer bias, and individual spatial overlap is erased by using binomial data.

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## 4.1 Density dependence, elevation, vole abundance and fluctuations

First-order negative feedback was the dominating density dependent structure in the pine marten time series. My findings therefore suggest that the pine marten population in Hedmark is direct density-dependent, and not cyclic (Berryman & Turchin, 2001). This is consistent with a study from Ontario, Canada, where snowshoe hares were the driving force, a temporal cohort analysis showed that the American marten displayed no short term cyclicality in population abundance, and displayed a density dependent growth (Fryxell et al., 1999). Zalewski and Jedrzejewski (2006) found that the pine marten densities in Poland were positively correlated with rodent abundance the previous year, and the authors suggest that the pine marten populations are not direct, but inversely density dependent. However, it is important to note that the study area is from central-Europe, where the bank voles are the dominant species in temperate forest, and are considered to be more stable in terms of abundance than microtus voles (Lanszki et al., 2007). In my study, the degree of density dependence was however negatively associated with both elevation and vole fluctuations, indicating that these two variables decrease the direct density dependence and potentially have a stabilizing effect on the pine marten population dynamics. This is not evidence that the marten population is cyclic but can indicate that they are more dependent on voles in their diet at increased elevation.

The degree of direct density dependence in the pine marten population was negatively associated with elevation. Elevation is a proxy of productivity and latitude, both of which are heavily correlated with elevation in Hedmark. Furthermore, pine marten abundance is positively correlated with vole abundance. The direct density dependence was negatively associated with variation in vole abundance. This might be due to less alternative prey, signifying an increased reliance on voles as sustenance (Vulla et al., 2009). Stronger amplitudes of vole peaks and lows can be found at higher elevations as well (Andreassen et al., 2019), and can maybe have a stronger effect on marten dynamics than in the southern lowlands in Hedmark. Latitude might also affect the search time for martens hunting voles, as lower ecosystem productivity and less alternative prey might prolong the search (Kleef & Wijsman, 2015; Zalewski et al., 2004), as a functional response. However, this does not mean that pine martens are obligate vole consumers at higher elevation. Zalewski (2005) highlighted how throughout Europe, the marten diet varies with latitude and puts an emphasis on the importance

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of microtines, and how martens respond functionally to increasing vole numbers. However, that study also suggests that microtines is less important in the northernmost part of its distribution area, and that birds such as capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*), willow grouse (*Lagopus lagopus*) and hares (*Leporidae*) become more important, especially if vole abundance is low (Zalewski, 2005). In Northern Finland, pine martens are more dependent on voles (Pulliainen & Ollinmaki, 1996), and incidentally also consumes larger prey such as the mountain hare (*Lepus timidus*). This is partly contradicted by another study from Finland using snow tracks as indices for predator abundance, suggests that mountain hares might not be as important for the martens diet (Kauhala & Helle, 2000). While the marten is affected by low vole years, they switch over to and supplement their diet with available prey (Wijsman, 2012) and food caching. Small rodents are an important source of sustenance for pine marten, since they also prey on squirrels and hunt arboreous (Helldin, 2000). During winter, the pine marten is observed retrieving cached food such as eggs, passerines, small mammals and amphibians. The caching of food might reduce the dependency on voles as a food source, as well as time spent foraging (Twining et al., 2018; Willebrand et al., 2017). A study investigating the seasonal variance in pine martens diet in a mountainous region in Spain, showed that the pine marten had a stable diet of microtines, regardless of prey abundance availability (Rosellini et al., 2008). However, that study was conducted in a region where fluctuations in vole abundance is not cyclic. In Fennoscandia, martens are not following the fluctuation in vole abundance as closely as the stoat and weasel, who are considered to be vole specialists (Korpimäki et al., 1991), and it seems it is not limited by access to food. Their reproductive biology with delayed implantation, and the late sexual maturation (Helldin & Lindström, 1995; Larroque et al., 2015), might be a mitigative factor against vole cycles, as these factors can regulate population growth. A study from Netherlands found that changes in vole abundance was positively associated with the variation in marten litter size (Kleef & Wijsman, 2015), the variation was still low, indicating that the marten litter size is not strongly affected by variation in abundance. It is important to mention that most of the literature are from temperate or Mediterranean regions, or from North America, and one must be aware of this when comparing these systems. However, the overall findings in the articles mentioned supports my results that the pine marten population dynamics differ on an elevational scale and is positively associated with variation in vole abundance. Furthermore, my findings that the pine marten abundance is also positively

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associated with vole abundance, is supported by several articles, strengthening the assumption that pine martens are dependent on voles.

Furthermore, another intraspecific regulator can be territoriality. It is important to mention that while territoriality can function as a regulator, there are still species who are both cyclic and territorial (Hanski et al., 1991), and this intraspecific behavior does not necessarily warrant a stable population (Fryxell et al., 1999). However, Pine martens are highly territorial with high fidelity towards their home ranges, (Zalewski & Jedrzejewski, 2006) with little overlap between males. Territoriality regulate population growth, as by defending a territory, an individual secures access to resources such as food, refuge and breeding partners, and prevents others from using these resources (Smith, 2015). The pine martens territorial structure consists of one male territory overlapping several female territories. Being territorial, and antagonistic in encounters with intruders, it might function as a regulator of the population, since transient pine martens that have not yet established territories have a lower chance of survival without suitable habitats to defend (Zalewski & Jedrzejewski, 2006). While there has been little research specifically on how territorial behavior in pine martens can regulate their population sizes, an article investigating territoriality and population growth in general, suggests that territoriality can increase population stability (Lopez-Sepulcre & Kokko, 2005), as aggressive interactions between territory holders can be a regulating and stabilizing factor, limiting growth by interspecific hostile interactions (Fryxell et al., 1999). Territorial behavior in pine marten can potentially regulate their numerical response to varying food access because habitats that are saturated with territories can force excess individuals into inferior habitats or to emigrate and become transient, thus lessening the predation and competition in a local area (Zalewski & Jedrzejewski, 2006). The territorial behavior of pine martens can function as mitigator against vole fluctuations, due to how limited space and territorial defense, in turn can limit growth, and work as a stabilizing factor, thus regulating the pine marten population.

## 4.2 Snow depth & settlement density

My results show that snow depth was positively correlated with pine marten abundance and density dependence, indicating that snow depth is a destabilizing factor for pine marten population dynamics. A previous study based on the same data set support the positive relationship between snow depth and pine marten (Cano-Martínez et al., 2021). Snow depth

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might also have an indirect positive effect on pine martens, as their competitor, the red fox, is more limited by snow depth, and tend to prefer areas with less snow (Selås & Vik, 2006). The red fox kill pine marten and might limit its abundance in areas shares by both species (Lindström et al., 1995), but pine marten abundances are not significantly affected by interactions with the red fox (Kurki et al., 1998). While the pine marten is also partially limited by increased snow depth (Jędrzejewski et al., 1993), this does not necessarily mean that the pine marten is forced out into subpar areas, as their small body size and weight might be beneficial for traversing through snow in a more efficient manner than the red fox (Selås & Vik, 2006). A Finnish study found that the pine marten takes advantage of the subnivean zone, by using areas with less snow (close to trees, fallen logs etc.) in order to gain access to its prey (Pulliainen & Ollinmaki, 1996). My findings, supported by previous studies, seems to be in the same direction, showing a positive association between pine marten and snow depth, possibly due to its adaptation to finding prey both above and under the subnivean zone in addition to avoiding competitors.

Pine marten abundance was negatively associated with settlement density in Hedmark, where the human population density is relatively low ( $6.9/\text{km}^2$ ). Pine martens are strongly attached to woodlands, and the presence of woodland patches is a requirement for the pine marten (Pereboom et al., 2008). While several studies have shown that pine martens avoid heathlands, clear-cuts, agricultural landscape and open areas, (Brainerd & Rolstad, 2002; Lombardini et al., 2015; Storch et al., 1990; Stringer et al., 2018), a study from Italy (Balestrieri et al., 2016) highlighted the importance of corridors in a fragmented landscape, and how pine martens utilized residual forests, hedgerows and riparian hedgerows to disperse (Pereboom et al., 2008), this effect was however negligible with an increased degree of anthropogenic disturbance (Balestrieri et al., 2016). Pine martens prefer areas with access to refuges, and seldom stray too far from forest habitats (Pereboom et al., 2008), and areas with a high degree of settlement density might not have the necessary prerequisites for maintaining a pine marten population. Studies of American martens relation to roads (Robitaille & Robitaille, 2000) states that they do not significantly decrease the habitat quality for martens, but significantly decrease dispersal. Similar studies from France suggests that they are not a complete barrier (Larroque et al., 2016; Pereboom et al., 2008), and can adapt to live in fragmented landscapes. Road density or frequency were not used as predictor in this study, but it is reasonable to assume that density of roads increases with increased settlement density. Furthermore, a study from

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Switzerland (Weber et al., 2018) investigated the distribution of pine marten in a heavily fragmented suburban landscape, and while the pine marten abundance was negatively affected, the article suggested that they can possibly adapt to live in areas with anthropogenic disturbances. The articles mentioned all supported my findings to some degree, that pine martens were negatively affected by settlement density. However, establishing and maintaining corridors and refuges might reduce the vulnerability of pine martens in relation to human impacts.

My findings indicate that the pine marten is not cyclic and displays a strong degree of density dependent population growth. Variation in vole abundance and elevation were stabilizing factors, while snow depth strengthened the degree of density dependence. The marten's functional response to varying access to prey, and intraspecific regulation can explain the perceived robustness of the specie. The marten abundance was lower in areas with a higher degree of settlement density, indicating that they are somewhat vulnerable to anthropogenic impacts, other studies suggest that they might adapt to live in areas with human activity. Marten abundance was positively associated with previous years vole abundance, suggesting that they are generalists, who are dependent on voles. The pine marten is an adaptive omnivore equipped with several strategies to mitigate the effect of vole cycles. They are adept hunters who adapt to changes in prey availability and are not as limited by environmental factors such as snow depth, as their competitor, the red fox. I recommend that in further studies the age- and sex composition, mortality and natality, variables such as roads, forest cover and squirrel density should be considered as potential variables. Another landscape variable that would have been interesting to look at would be forest cover, forest type and clear-cuts. However, these data are not updated regularly, and thus cannot be implemented as a variable in our models without being inaccurate. Additionally, a longer time series is needed in order to increase the resolution of the data and strengthen the predictive power of the models for detecting cyclicality.

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