Fuzzy Neighbours or Hairy Enemies

Assessing habitat use in central and northern Sweden using camera traps on pine marten and red squirrel

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Abstract

The pine marten (*Martes martes*) and Eurasian red squirrel (*Sciurus vulgaris*) are old forest specialists in Sweden, experiencing historic and current population declines, possibly due to climate change and habitat loss. However, studies have shown mixed results regarding pine marten predation on red squirrels. Earlier theories suggest that the marten is thought to have evolved specifically to hunt red squirrels, even though its current main food source is other small rodents.

Camera trap data was utilised from two areas in boreal Sweden, collected over seven months from September to March. Cameras were baited with peanut butter to identify individual martens in another project. There were a total of 1290 pine marten, 687 small rodent and 29 red squirrel observations. A time until the first event was recorded for each camera, along with the average tree height, standard deviation of tree height, and the proportion of trees under 6 m, in a 50 m radius around the camera, were included as variables. Intraspecies spatiotemporal interactions between marten and red squirrel, as well as between small rodents and marten, were analysed. Tree height significantly shortened the time until first detection for rodents and pine martens, but not for red squirrels, while the other factors had no significant effect. Earlier literature suggests that both rodents and martens favour older forests, possibly due to better shelter and thermal protection provided by these habitats. A higher chance of detecting rodents after marten observation was found, but no significant effect for squirrels. Martens were more likely to be observed shortly after squirrels and rodents. Martens likely follow the other species due to predation. The few squirrel observations could be because of strong avoidance of martens, obscuring the true response, as martens were observed at 45 out of 53 cameras. The apparent disregard of rodents towards their predator may stem from their exposure to many different predators, making it impossible to evade all threats, or possibly an attraction to the bait, which might also affect the squirrels. The conclusions, therefore, are that clearcuts in forestry create worse conditions for the pine marten and rodents, while more pine marten might be worse for the red squirrel, which might make it necessary to adapt forestry practices in the future.

Keywords: Time to first event, Land cover, PAMM, Wildlife, Species Interactions, Boreal Forest

Table of contents

List of tables

List of figures

Abbreviations

CT	Camera trap
PAMM	Piece-wise exponential additive mixed model

1. Introduction

Anthropogenic land-use affects most, if not all, ecosystems worldwide, in various forms, such as urbanisation, deforestation, or agricultural land use (Bürgi *et al.* 2017). The boreal forests of Sweden have been affected by industrial forestry since at least the early 20th century, reducing the amount of natural disturbances and changing the natural structures (Linder & Östlund 1998; Josefsson & Östlund 2011). In Sweden, many mammals are generalists, in terms of habitat usage, such as the red fox (*Vulpes vulpes*), the badger (Meles meles) and many rodents (*Rodentia spp.*). However, the European pine marten (*Martes martes*) and the Eurasian red squirrel (*Sciurus vulgaris*) are two exceptions that are known to rely on old-growth forests in the northern part of their range (Andrén & Delin 1994; Kurki *et al.* 1998). The effect forestry has on these old-growth forest specialists can be detrimental, and long-term monitoring is essential to understand these effects (Theobald *et al.* 2011).

1.1 Species of interest

The Eurasian red squirrel is a small tree-dwelling mammal commonly seen in forests, parks and other wooded areas all across Eurasia (Cánovas *et al.* 2015). Although it is found in both fragmented landscapes and urban areas, it prefers older spruce forests and struggles when clear-cut areas become too prominent (Andrén & Delin 1994; Michał & Rafał 2014). Its main food source is coniferous and broadleaved seeds, but may also be supplemented by fungi and insects (Krauze-Gryz & Gryz 2015). Common predators of squirrels include birds of prey such as goshawks, sparrowhawks, and tawny owls, as well as mammalian predators, mainly the pine marten (Randler 2006). Certain forestry practices, mainly small clearcuts, have been shown to increase some rodent populations, which in turn increases the food availability for predators. (Niemi & Hanowski 1997). This increase in predator populations might also be one of the reasons for reduced squirrel populations at high enough clear-cut densities. Recently, the spread of adenovirus has become an emerging threat to the red squirrel populations (Everest *et al.* 2014). However, the primary threat to the red squirrel remains the invasive eastern grey squirrel (*Sciurus caroliensis*), especially on the British Isles and Italy, where it competes with the red squirrel and has caused local extinction (Gurnell *et al.* 2004).

The pine marten is a small mesocarnivore distributed across Europe and is seen as a food generalist but a habitat specialist (Herrero 2016). Its main food source is small rodents, but it may also include insects, squirrels and birds (Pulliainen & Ollinmaki 1996; Helldin 2000b; Petrov *et al.* 2016). The marten is generally considered an old-growth forest specialist in its northern range and is thus negatively affected by human land use (Kurki *et al.* 1998). It has a lower preference for agricultural lands compared to other mesocarnivores such as the red fox, which might be caused by its high chance of predation in open areas (Kurki *et al.* 1998; Randler 2006; Cano-Martínez *et al.* 2024). The pine marten instead thrives in habitats that provide structural complexity, which are more common in older forests, such as snags and arboreal cavities which serve as both foraging sites and shelter (Lapin 2005; Angoh *et al.* 2023). These structures are critical for reducing predation risk from species like red fox, with which the marten shares its range (Brainerd *et al.* 1995). Some rodents are more common in wooded areas as compared to clearcuts, increasing the available food for the marten (Hansson 1989). Both the high-intensity forestry conducted in Sweden and historic hunting by humans have, in periods, greatly reduced the marten populations to near extinction, with one large decline in the early 20th century and another one later in the same century (Helldin 2000a; Angoh *et al.* 2023).

1.1.1 Red squirrel and pine marten interactions

Historically, pine marten has been known to prey on the red squirrel, but generally not at a large scale, especially uncommon in southern and western Europe, with a more frequent predation in boreal Russia (Sheehy & Lawton 2015). As previously mentioned the main threat to the red squirrel is the invasive grey squirrel, and therefore most studies on pine marten-red squirrel interaction are conducted in the invaded areas, where there is a positive correlation between pine marten and red squirrel (e.g. Sheehy & Lawton 2014; Sheehy *et al.* 2018; Twining *et al.* 2021). Caravaggi *et al.* (2018) saw an overlapping activity pattern of squirrels and pine martens, indicating interactions, even though they did not differentiate between the European red squirrel and eastern grey squirrel. This has generally been explained by the low chance of predation of the red squirrel by pine marten, while the grey squirrel has a higher chance of predation from the same predator. However, the red squirrel has also shown a slight decline in areas not invaded by the grey squirrel, namely northwestern Russia and Finland, instead, the decrease is probably due to a warmer climate (Turkia *et al.* 2018b).

Few studies have been conducted in the boreal forest on pine marten and red squirrel interactions. Bottom-up drivers have been found to drive the red squirrel population size, with seed availability affecting the squirrel population. However, no interaction between pine marten populations and red squirrel populations has been found in previous studies (Pulliainen 1984). There are few instances found of pine marten predating on red squirrel, suggesting a weak interaction between the two species (Pulliainen 1984). Cano-Martínez et al. (2024) found a stronger correlation between land coverage and mesocarnivore sightings compared to large predator sightings and mesocarnivores. This indicates a bottom-up control in these ecosystems as well, which means available prey, other than red squirrels, dictates the population of the marten and not top predators. It has also been speculated that the red squirrel and pine marten have co-evolved and that the red squirrel in this instance has a strong response to avoid predation from the pine marten, even though few squirrels are predated (Twining et al. 2022). Despite the suspected co-evolution, the martens most common food source is other small rodents such as voles and mice. It is therefore important to also consider rodent-marten interactions when investigating squirrel-marten interactions.

The interaction between red squirrel, grey squirrel and pine marten has been investigated heavily in areas where all three species are present. However, few studies have been investigating only pine marten and red squirrel interactions, apart from showing limited predation (e.g. Storch *et al.* 1990; Jędrzejewski *et al.* 1993; Sheehy *et al.* 2018). The decrease in red squirrels caused by invasive species, disease and climate change needs to be considered and investigated in a system where the invasive grey squirrel is absent for us to know the possible implementation of the pine marten as a tool to combat the extinction. The historically low marten populations also give credence to further research into the species and monitoring.

1.2 Aim and research questions

This thesis aims to investigate both habitat use by pine marten, red squirrel and small rodents, as well as spatial-temporal interactions between the same species using camera trap (CT) data. Specifically, the study examines how the recent presence of one species influences the detection of the other, and how forest structure and human land use affect martens' habitat use. Further, additional research on the effect of human land use on martens and red squirrels in northern latitudes is needed, as it is currently largely absent from the existing literature. Both the historic small population of marten and current threats to the red squirrel are still cause for concern and warrant further research. Cano-Martínez *et al.* (2024) highlight the importance of considering anthropogenic disturbances when investigating species interactions. Differences in both species' range have been somewhat investigated in earlier studies on the species individually (see Cano-Martínez *et al.* 2024). However, the interactions between the pine marten and the red squirrel in the boreal forest and Sweden are not that well studied. Few studies have been conducted on both species north of the Grimsö research station in Sweden. This study therefore aims to answer the following questions:

- Does the red squirrel avoid places recently visited by the pine marten?

- Is the pine marten more likely to visit places recently visited by the red squirrel or small rodents?

- Does the nearby tree height affect the time until first pine marten, red squirrel or small rodent detection?

2. Method

2.1 Research area

This study investigated CT data from two areas, Grimsö research station in Örebro county and Kulbäcksliden research forest in Västerbotten county. Kulbäcksliden is an experimental forest in the boreal zone established in 1923 and part of the Svartberget research station. The experimental forest has an elevation of 160-320 m above sea level and is dominated by Norway spruce and Scots pine forest with a mean annual temperature of 1.8º C and a mean precipitation of 614 mm (Lindgren 2024). Grimsö research station is in the hemiboreal zone, has a mean elevation of 118 m above sea level, a mean annual temperature of 4.7º C and a mean precipitation of 739 mm (SITES 2025).

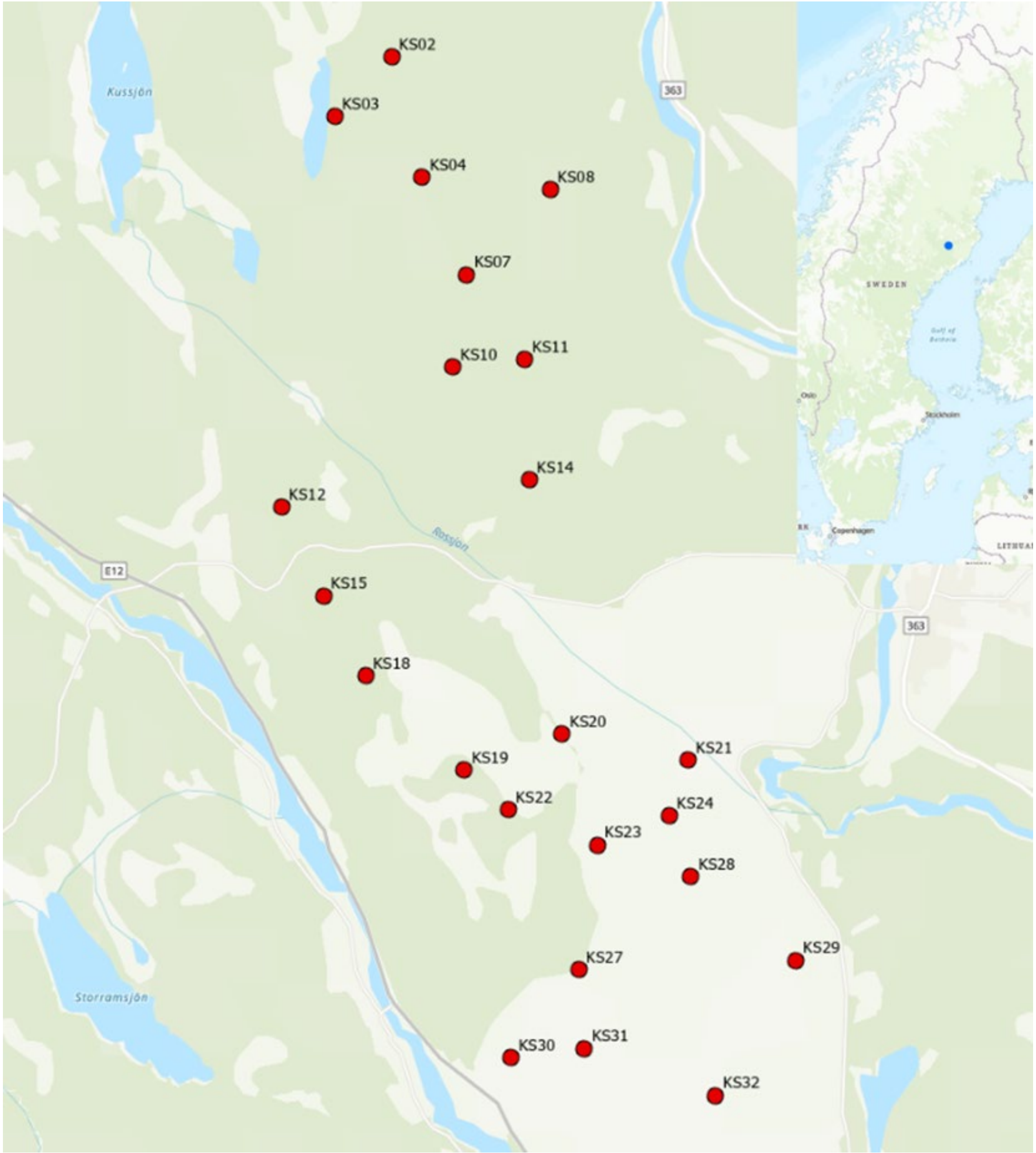

Figure 1: Camera locations at Kulbäcksliden, Västerbotten county. The red dots represent the location of each camera trap.

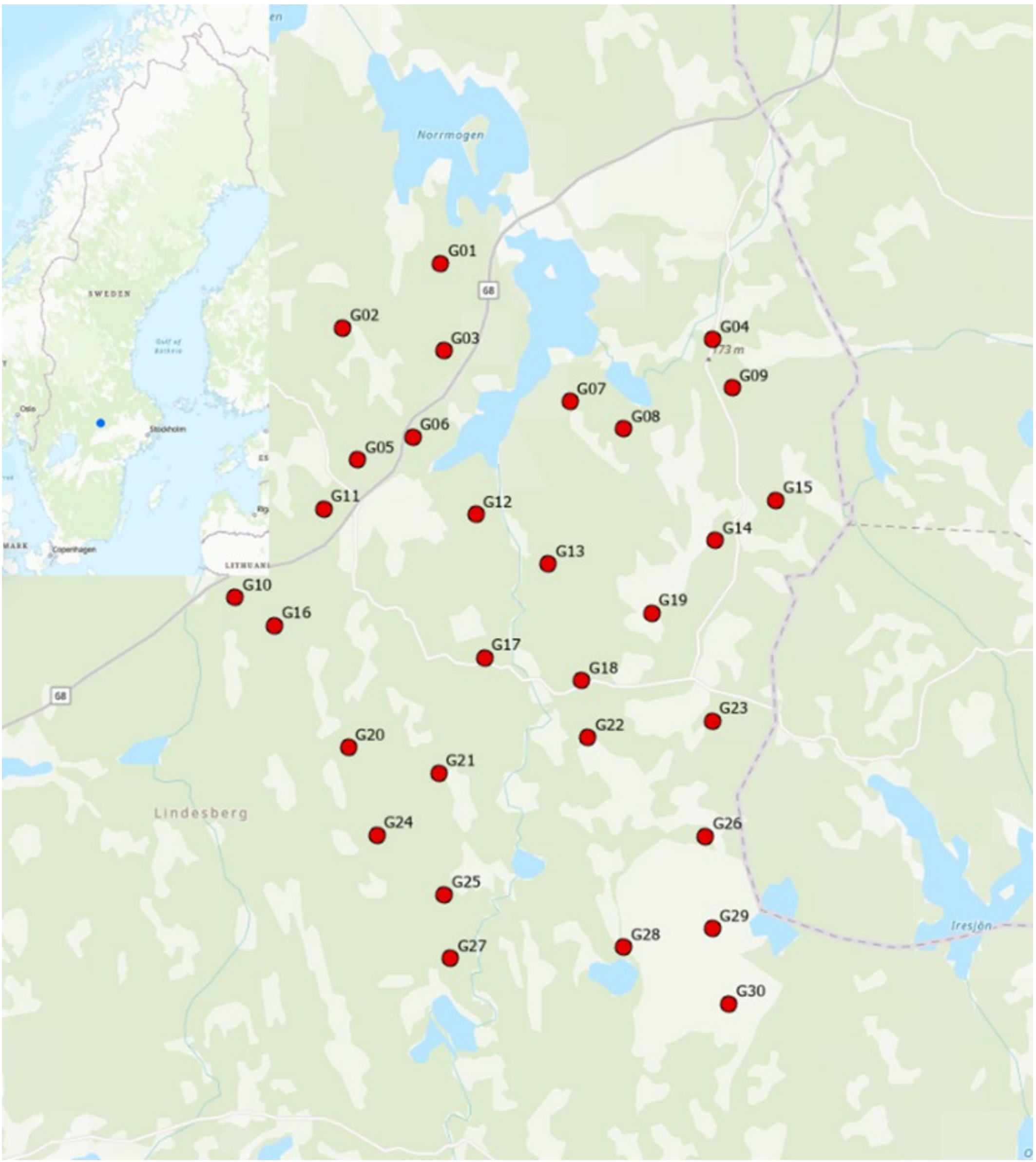

Figure 2: Camera locations at Grimsö, Örebro county. The red dots represent the location of each individual camera trap.

2.2 Camera traps

In total, 53 Reconyx HyperFire2 movement-activated CTs were used, 30 in Grimsö and 23 in Kulbäcksliden. They were out from July 30 2024 until March 13 2025 for a total of 227 days, with some differences between the cameras due to it taking multiple days for setup and delays in permissions from some landowners in Kulbäcksliden. Each CT was pointing towards a wooden frame roughly 1m x 0.6m across fastened approximately 1.3m above the ground, with a jar of peanut butter hanging slightly below the top frame to attract pine martens. The peanut butter, batteries and memory cards were changed at the beginning of November, halfway through the sampling period. The cameras were set to the following settings:

- Sensitivity set too high.
- Movement activation triggers a 3-second video sequence.
- Sequences are prolonged when the camera continues to register movement into > 3-second videos.
- Each sequence is combined into one observation if they are within 5 minutes of each other.
- Infrared flash is activated.
- Every 24h one picture was taken to check for camera functioning.

2.3 Data analysis

Each video sequence was manually categorised on the TRAPPER project website (Bubnicki *et al.* 2016) by the author and was approved by supervisors. The Excel file that was created was analysed in R (V. 4.4.2). In ArcGIS Pro (V.3.3.1) raster land cover data from the Swedish Nature Protection Agency (Naturvårdsverket 2025) and raster tree height data from the Swedish Forest Agency (Skogsstyrelsen) was used as a substitute for land usage and forest age, respectively. Each raster had a cell size of 10x10m as its highest resolution. Around each CT, a buffer zone with a radius of 50m was calculated. Within this buffer zone, only land cover expected to have trees was used (Table 1). All land covers not expected to ever have a tree cover were removed from the analysis, such as roads, agricultural lands and open mires.

Table 1: The cover type used in each research area.

Forest type	**Grimsö**	**Kulbäcksliden**
Pine forest on dry soil	x	x
Spruce forest on dry soil	x	x
Mixed coniferous forest on dry soil	x	x
Mixed forest on dry soil	x	x
Thin-leaved deciduous forest on dry soil	x	x
Broadleaved deciduous forest on dry soil	x	-
Clearcut	x	x
Pine forest on wetland	x	x
Spruce forest on wetland	x	x

Mixed coniferous forest on wetland	x	x
Mixed forest on wetland	x	x
Thin-leaved deciduous forest on wetland	x	x

2.3.1 Forest height and time until first marten detection

To account for the fact that bait was used, only the time until first detection could be used as a proxy for marten, squirrel and rodent activity and density. Subsequently, a Cox proportional hazards model was used where survival was counted for each camera until its first detection of each species with the package survival (V.3.6-2) (Cox 1972; Therneau 1990). Each CT, therefore, had a timestamp for the start of the survey, the first detection and the end of the survey. Thus, a detection delay was calculated in days. For CTs with no detections, the delay was the end of the survey and marked as 0, while the ones with observations were marked as 1 and the timestamp for the observation. From this, the Cox proportional hazards models were created, which included site, mean tree height, standard deviation in mean tree height and the proportion of area within the buffer with trees under 6m. For the squirrel and rodent models, the site was not used as there were too few observations of these species to divide them any further. A Log-rank test was done to compare the difference in time until first marten detection between the sites. To visualise the model, the package survminer (V.0.5.0) was used. (Kassambara et al. 2016)

2.3.2 PAMM analysis

To investigate the temporal relationship between the red squirrel and pine marten, a piece-wise exponential additive mixed model (PAMM) was used through the package ctrecurrent (V.0.1.0) (Ferry *et al.* 2024) and pammtools (V.0.7.3) (Bender & Scheipl 2018) with code adapted from Ferry *et al.* (2024). This allows for an analysis that investigates how the primary species temporally affects the secondary species; this effect can be either attractive or repulsive, if at all present. PAMM can use data that has a large discrepancy in the number of observations between species (Ferry *et al.* 2024). All observation that happened within five minutes of each other was combined into one event to account for animals staying for more than one video sequence. One analysis was done for each pair of species in Table 2. Due to difficulties in deciding species for small rodents, all rodent observations for these species were combined into the order *Rodentia*.

Table 2: The primary and secondary species of the analysis

Primary Species	**Secondary species**
Marten	Squirrel
Squirrel	Marten

Marten	Rodent
Rodent	Marten

A time-to-event survey was created, which started a survey after the primary species was detected and ended either after the secondary species was observed or when 30 days had passed, after which no effect of the primary species should be expected to remain. The surveys were transformed into a time-to-event format, breaking down the survey into smaller time intervals. This allows for modelling of the changes in the likelihood of seeing the secondary species after the primary using PAMM. The difference in setup time for each CT was accounted for.

3. Results

Pine martens were detected at 45 out of 53 CT stations, with 1,290 marten observations. Red squirrels were recorded 29 times across 8 CT stations, while small rodents were detected 687 times at 34 CT stations. The forest tree height affected the time-to-first marten detection rate, which decreased with tree height ($p=0.04$) and time-to-first detection for rodents, which also decreased with tree height ($p = 0.01$). Standard deviation in tree height and proportion of area with trees under 6m did not significantly affect the time until first detection. Based on the marten, squirrel and rodent observations, a temporal association was detected in 3 out of 4 primary and secondary species combinations, the only exception being marten as primary species and squirrel as secondary species.

3.1 Forest height and time until first marten detection

The Log-rank test shown in Figure 3 found a significant difference in the rate at which cameras detect marten between the two sites, with faster detection rates at Kulbäcksliden ($p = 0{,}002$). In Kulbäcksliden, 20 out of 23 CTs detected marten at least once during their deployment, while 25 out of 30 CTs at Grimsö detected marten. The Cox proportional hazards model shows a 3,7 times higher risk of detection at Kulbäcksliden but no difference in the standard deviation of tree height or the proportion of trees under 6 m ($p = 0{,}53$ and $p = 0{,}64$ respectively), shown in Table 4. Mean tree height showed a positive and significant trend toward faster marten detection ($p = 0{,}04$). This effect was larger in Kulbäcksliden than in Grimsö (Figure 3).

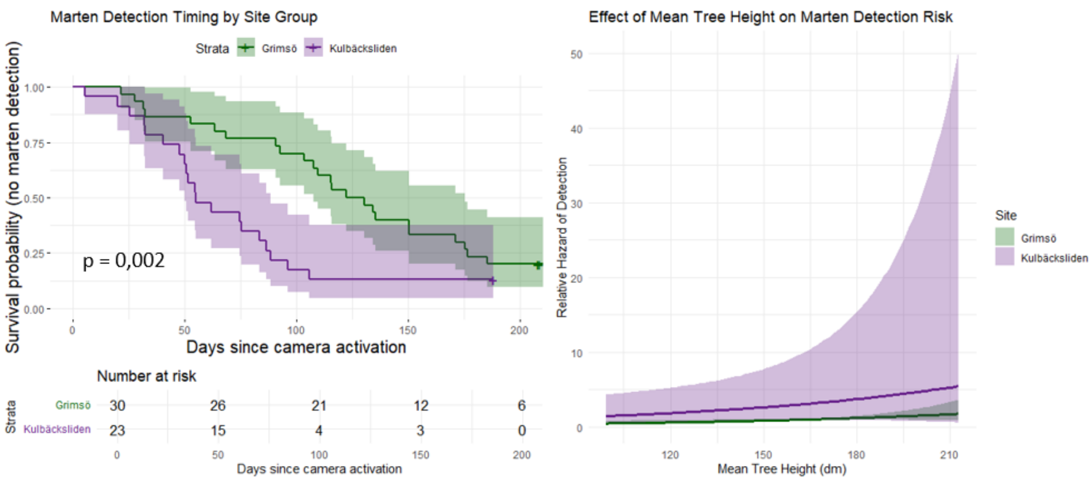

Figure 3: The left figure shows the probability of no marten detection for both Grimsö (green) and Kulbäcksliden (purple) since CT deployment, p = 0,002 indicates a

significant difference in marten detection between the sites. The table shows the number of CTs with no marten detection since the first deployment. The right figure shows the effect of mean tree height on the time until the first marten detection for both sites.

Table 3: Cox model summary table for time until first marten detection, n = 53, 45 events.

Predictor	Coefficient	Hazard Ratio	Std. Error	z-value	p-value
Site: Kulbäcksliden	1.13	3.11	0.35	3.26	<0.001
Mean tree height	0.01	1.01	0.01	2.01	0.04
SD tree height	0.02	1.02	0.02	0.62	0.53
Proportion under 6m	4.41	82.21	9.44	0.46	0.64

Time until the first rodent detection was only significantly affected by mean tree height (p = 0.01), with a faster detection rate at higher tree heights (Table 4, Figure 4).

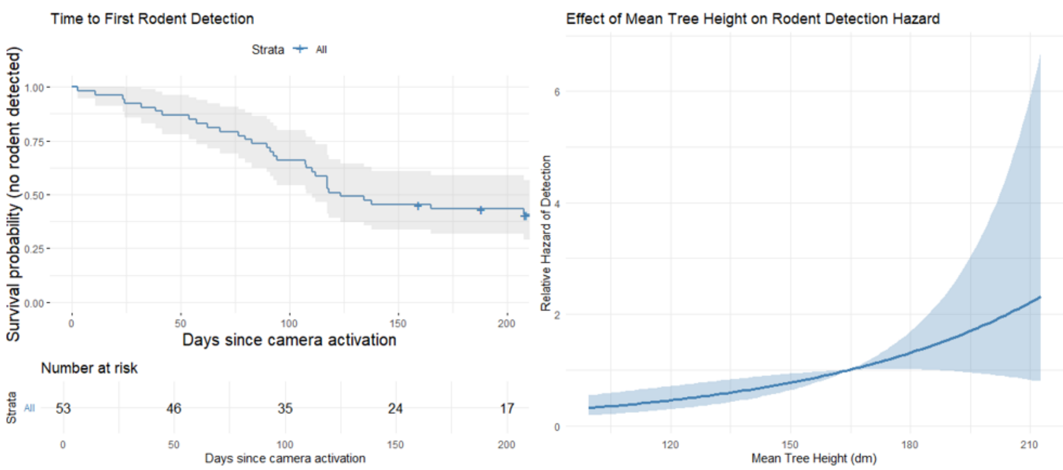

Figure 4: The left figure shows the probability of no rodent detection since CT deployment. The table shows the number of CTs with no rodent detection since the first deployment. The right figure shows the effect of mean tree height on the time until the first rodent detection.

Table 4: Cox model summary table for time until first rodents, n = 53, 34 events.

Predictor	Coefficient	Hazard Ratio	Std. Error	z-value	p-value
Mean tree height	<0.01	1.02	<0.01	2.52	0.01
SD tree height	0.02	0.98	0.02	-0.78	0.43
Proportion under 6m	11.98	1.5*10^5	8.21	1.46	0.14

Time until first red squirrel detection was not significantly affected by any of the factors tested, with too few observations to include site as a factor, due to the low number of CTs detecting squirrels (Table 5).

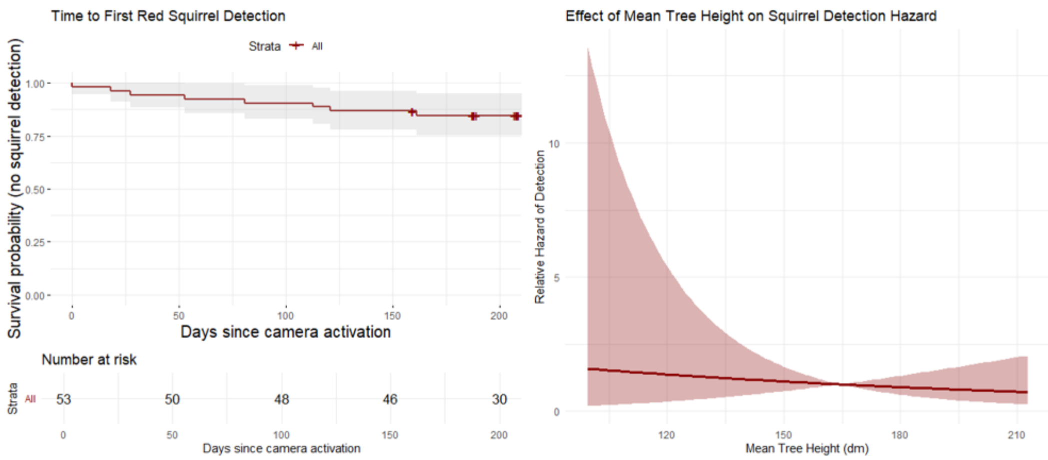

Figure 5: The left figure shows the probability of no squirrel detection since CT deployment. The table shows the number of CTs with no squirrel detection since the first deployment. The right figure shows the effect of mean tree height on time until first squirrel detection.

Table 5: Cox model summary table for time until first squirrel, n = 53, 8 events

Predictor	Coefficient	Hazard Ratio	Std. Error	z-value	p-value
Mean tree height	<0.01	0.99	0.01	-0.47	0.64
SD tree height	0.04	1.04	0.04	0.86	0.39

Proportion under 6m	2.72	15.15	15.01	0.18	0.86

3.2 PAMM analysis

All primary-secondary species combinations showed a pattern over time in the likelihood of species occurrence after the other species occurred (p <0.001) except for when marten was primary and squirrel secondary (p=0.4) (Table 6). There was no clear response of squirrels on pine martens (Figure 6d). For all other analyses, the estimated hazard was the highest shortly after the primary species was detected, indicating a peak in secondary species detection in the early part of the survey window. The one exception was when the squirrel was primary and the marten secondary, having multiple peaks. This was also the analysis with the highest level of deviance explanation (9.36%). Marten was significantly attracted to rodents, with marten being more likely to be observed immediately after a rodent detection (Figure 6a). However, the level of explanation was lower than that of the squirrel as primary and the marten as secondary (7.22%). Rodents were also showing some attraction to marten, although it had the lowest degree of explanation among the significant analyses (Figure 6a) (4.4%). Among all species combinations tested, the strongest temporal response was found when squirrels preceded marten (9.36%).

Table 6: Summary of PAMM analyses for the primary and secondary species

Primary→Secondary	edf	p-value	Deviance explained
Marten→Squirrel	1	0.428	1.16%
Squirrel→Marten	1	<0.001	9.36%
Rodent→Marten	1	<0.001	7.22%
Marten→Rodent	1	<0.001	4.4%

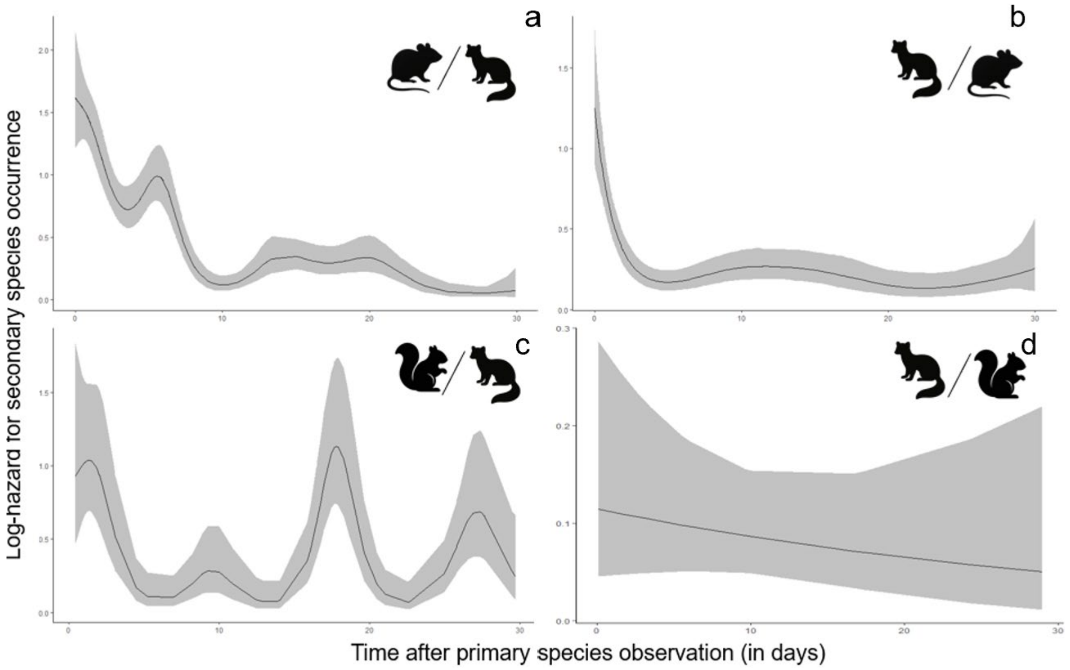

Figure 6:A PAMM analysis for all combinations of primary/secondary species, which can be seen as the figures in each corresponding graph. Graph (a) has rodents as primary and marten as secondary, graph (b) has marten as primary and rodents as secondary, graph (c) has squirrels as primary and marten as secondary, and graph (d) has marten as primary and squirrels as secondary.

4. Discussion

Understanding predator-prey spatiotemporal dynamics is essential for understanding habitat use and wildlife behaviour in managed landscapes. This thesis investigated CT data for one autumn and winter season in two locations in boreal Sweden, focusing on squirrel and marten interactions. It investigated their interactions on a temporal scale for avoidance or attraction of one another, as well as for small rodents and marten interactions, to better understand how the marten interacts with its prey.

While there was no significant evidence that marten affects squirrels in any way, the data suggests that the reverse is true, with squirrels attracting marten directly following squirrel visits. Both the marten and the rodents attracted each other shortly after a visitation. This thesis found evidence suggesting a preference for martens and small rodents in forests with higher tree cover, but no preference for tree height in squirrels. The extremely low number of squirrel observations could be caused by a strong avoidance of the pine marten, making the high number of marten observations mask the response of the squirrels.

4.1 Forest height and species activity

The response to forest height for pine marten is described in the literature, where it is established that the species is a forest specialist, especially in the boreal forest (e.g. Kurki *et al.* 1998; Herrero 2016; Angoh *et al.* 2023). A higher presence of martens is thus expected in areas with old-growth forests. This study can however not discern between a higher population of martens or a preference for individual martens at sites with higher trees, or if it is a combination of both. Even though the rodents were not classified on a species level, many were likely bank voles (*Clethrionomys glareolus*), which are most commonly found in forested areas (Kauer *et al.* 2024). Rodents have also been found to prefer forests as opposed to open clearcuts, both in this study and in existing literature, although some species are more common in agricultural lands (Hansson 1989). This was further supported by the findings in this study. No significant effect was found in the standard deviation of forest height in any species. The forest provides protection from some avian predators as well as protection from the cold temperatures during winter. Erlinge *et al.* (1983) found a clear link between tree diameter at breast height and how stable the night temperature was in cavities within the tree, with a higher temperature during the night in larger trees. Therefore, pine marten and rodents might prefer larger trees in colder areas, where protection from the elements is needed. This has been suggested to be one of the reasons pine martens prefer older forests, especially in their northern range (Brainerd *et al.* 1995).

To draw more certain conclusions, another study aimed at looking directly at how these species respond to forest age or height might be needed. If more evidence also suggests that older trees are important, conducting forestry with small mammals in mind might be needed. Although Sweden has a stable population of marten, and forestry might not need to be adapted with the species in mind, other countries in the animal's range have both seen a decline and reintroduction of marten. There are efforts for reintroducing and strengthening the pine marten populations in Britain, where the need for suitable habitat is one of the main limiting factors, with the lack of tree-covered areas is one of the main concerns (MacPherson & Wright 2021). Other studies have found a preference for tree cover over open fields in Italy (Manzo *et al.* 2012). This partially supports the findings of a preference for higher trees found in this thesis in other parts of the pine marten's range. However, the lack of areas with no tree cover in the study area makes the comparison difficult to make.

4.2 Pine marten, red squirrel and rodent interactions

The interactions between the marten and the squirrel only found a significant attraction from the squirrel towards the marten, with a higher chance of marten observation directly following a squirrel visit. There are multiple peaks in the marten observations after squirrel visits, with the later ones possibly caused by marten periodically visiting each site instead of an actual response to squirrels (Figure 6c). The strong response by marten on squirrel visits could give credence to marten predating on squirrel, as described in a multitude of studies (e.g Pulliainen 1984; Jędrzejewski *et al.* 1993; Pulliainen & Ollinmaki 1996). The findings in this study are somewhat opposed to Pulliainen (1984), who only found a weak interaction between the pine marten and red squirrel.

The interaction between squirrels and martens might be hidden behind the large number of pine marten observations that could lead to fewer squirrel observations, if squirrels spatially avoid martens. If this hypothetical response is too pronounced, it may significantly reduce the number of squirrel observations, rendering analysis impossible, as illustrated in this study with a total of 28 squirrel observations. Meanwhile, the interaction between rodents and martens can be explained by two distinct factors. Rodents serve as the primary food source for pine martens, which accounts for the attraction of martens to rodent observations (Pulliainen & Ollinmaki 1996). The attraction of rodents to pine martens may be influenced by the scent of peanut butter, which potentially disperses more after a marten has been present and fed on it. When comparing the number of predators preying on rodents and squirrels, the difference is evident, with rodents facing a greater number of predatory threats than squirrels (Erlinge *et al.* 1983; Turkia *et al.* 2018a). Apart from being hunted by martens, squirrels are mainly only hunted by certain avian predators, allowing them to avoid areas with higher risks of predation. The larger number of predators faced by rodents may compel them to tolerate a greater level of danger, as they would otherwise struggle to find resources. Due to martens' attraction to rodents and rodents' attraction to martens, the preference for high trees could pertain to just one of the species, while the interspecific attraction might create the illusion of preference for higher trees in the other species. However, the earlier literature suggests that the marten and the bank vole both prefer older forests, making it likely that the effect is seen in both species separately (Angoh *et al.* 2023; Kauer *et al.* 2024).

It is important to realise that using bait heavily affects how the species interactions can be interpreted. This is because the interactions are not directly between the species per se, but instead how one species affects the interactions between the other species and the bait. Rodents' apparent attraction to marten is a great example of this, where one would expect rodents to avoid predators, but the potential increase in bait attraction following a marten visitation results in a stronger response than predator avoidance. Therefore, baiting in CT studies is often more common when the species of interest is possible to individually identify for capture-recapture studies, especially for more elusive species and when estimating population sizes (du Preez *et al.* 2014). Baiting for predators has sometimes been shown to decrease the likelihood of also observing prey species, which could be the cause of few squirrel observations in this study (Rocha *et al.* 2016). Meanwhile, other studies have found no effect on prey species from using baits (Buyaskas *et al.* 2020).

4.3 Limitations

The original aim of the camera trap data was to investigate the ecology and family structure of martens, rather than comparing interactions among squirrels, rodents, and martens. Consequently, the camera trap locations were not completely randomly placed across the landscape, reducing their suitability for land cover analysis. Most cameras were also positioned near roads for ease of access. No CTs were placed outside older forests, and the amount of area with low to no tree height was low, making it difficult to know the exact response clearcuts have on these species. However, it is increasingly common to utilise CT data for purposes other than originally intended. For instance, Cano-Martínez et al. (2024) used CT data from the larger camera trapping project SCANDCAM (NINA 2024) when investigating mesocarnivores, their predators, and habitat structure. Hofmeester et al. (2019) further discuss the use of bycatch CT data for species not originally targeted by the study, while emphasising the importance of considering differences in detection probability between species.

The large disparity between pine marten and red squirrel observation numbers is problematic from a statistical point of view, with 1290 marten observations and 29 squirrel observations. However, the PAMM analysis was used because it is not as sensitive to large differences in the different species observations (Ferry *et al.* 2024). The similarity between habitat selection between both pine marten and red squirrel also implies a good suitability for a comparison between the species (Andrén & Delin 1994; Kurki *et al.* 1998; Hofmeester *et al.* 2019). As previously mentioned, the large difference in the number of observations might also be explained by an actual behavioural response by the squirrel that is strong enough to greatly reduce the chance of squirrel observation when pine martens are present.

4.4 Further research

To further assess the impact of human land use on both species, a wider variety of camera locations would be needed, such as having cameras not only in middle-aged to old-age forests. The effect of using baits in CT studies is often discussed in the existing literature, with it being a common approach for elusive species as well as species that are possible to individually identify (e.g du Preez *et al.* 2014; Rich *et al.* 2016). The aim of this study, however, was not to estimate population densities but to evaluate land use and species interactions. This means that the baits may affect the animal's behaviour, and to gain further knowledge of their interactions, a similar study without baits would be needed.

4.5 Conclusion

This thesis found evidence that both pine martens and small rodents prefer higher tree cover, but did not find any evidence that the red squirrel exhibits the same preference, indicating that forestry could have a negative impact on pine martens and small rodents. Furthermore, the thesis did not find evidence that areas with low tree height or variance in tree height affected any of the species studied. All investigated pairs of species interacted with one another to some extent. Squirrels attracted martens, but martens did not influence the behaviour of squirrels, whereas rodents and martens attracted each other. The interaction between squirrels and martens was influenced by the limited number of squirrel observations, which may be a result of a significant avoidance of martens by squirrels. The attraction of rodents following a marten visitation may be attributed to the marten distributing peanut butter scents, while martens typically prey on rodents. When considering the spatiotemporal interaction between the pine marten and the red squirrel, this thesis hypothesises that the interactions will generally be negative for the squirrel, as the available time and resources for the squirrel to gather resources are greatly diminished in the presence of martens. This result thus suggests that forestry with many clearcuts affects both pine marten and rodents, negatively affecting both the martens and rodents. Meanwhile, an increase in martens could negatively impact the red squirrel in the context of the boreal forest.

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Popular science summary

The pine marten and red squirrel have seen population declines in at least parts of their range, with the most current problem being the grey squirrel threatening the red squirrel in Britain and parts of Italy. As both animals are old forest specialists, loss of areas they live in and a warmer climate might be future problems in Sweden. Both animals have seen efforts to increase their numbers to try to combat the current decline. The European pine marten is a good predator against both the grey squirrel and small rodents, making it a valuable ally in restoring the red squirrel population. However, how the red squirrel and pine marten behave towards each other is somewhat complicated, because sometimes the pine marten eats red squirrels, but they also reduce the number of grey squirrels where they are present and therefore improve the chances for the red squirrel.

Videos from camera traps were collected in two different areas of Sweden, recording footage between September and March. The camera trap data that was used had peanut butter to increase the likelihood of observing martens to individually identify them. There were more observations of pine martens and rodents compared to squirrels. The time it took until the first of each species was detected by each camera was examined, along with how this time was influenced by forest height, fluctuations in forest height, and the extent of forest below 6 m in the direct surroundings of the camera. The interactions among pine martens, red squirrels, and rodents were also investigated. Taller trees (older forest) reduced the time until the cameras detected both martens and rodents, but did not affect squirrels. Fluctuations in forest height (variation in tree age) and the area comprising low forest (young trees) did not appear to influence any of the animals. The preference of martens and rodents for taler trees may come from the shelter they provide against the elements and predators. Rodents seemed to be attracted to martens, while martens appeared to be drawn towards both squirrels and rodents. Squirrels, however, were not influenced by the presence of martens. The attraction of martens to the other two species is likely due to their predatory behaviour towards them, while the rodents are probably attracted by the scent of peanut butter that is spread by the martens eating it. Squirrels might be so fearful of martens that the frequent visits by martens keep them away, making it difficult to see how afraid the squirrels are. The apparent lack of fear the rodents show toward martens could be because most predators prey on rodents, making it impossible to avoid every area visited by a predator without starving. Squirrels face fewer predators and may therefore be able to keep a safer distance. Because of these results, clearcuts are worse for the pine marten and rodents, while more martens are worse for the squirrel, maybe making it necessary to adapt forestry practices in the future.

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