

Voles and their trophic interactions in a changing landscape

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals. Articles I and II are reprinted with permission from their copyright holders.

- I Savola, S., Henttonen, H., & Lindén, H. 2013: Vole population dynamics during the succession of a commercial forest in northern Finland. — *Annales Zoologici Fennici* 50: 79–88.
- II Voutilainen, L., Savola, S., Kallio, E. R., Laakkonen, J., Vaheri, A., Vapalahti, O., & Henttonen, H. 2012: Environmental change and disease dynamics: effects of intensive forest management on Puumala hantavirus infection in boreal bank vole populations. — *PloS one*, 7: e39452.
- III Savola, S., Huitu, O., Sundell, J., Henttonen, H., & Lindén, H. The effects of top-down and bottom-up forces on red fox population. Manuscript.
- IV Holmala, K., & Savola, S. Avoiding predator or finding prey – habitat utilization and movements of red fox in relation to Eurasian lynx in southern Finland. Manuscript.

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- I Collected the field data, performed the data analysis and wrote the manuscript.
- II Collected the field data and samples, took part in the laboratory work and manuscript preparation. The article is also included in Liina Voutilainen's doctoral thesis.
- III Took part in the study planning, performed statistical analyses and wrote the manuscript.
- IV Took part in the field work, data analyses and manuscript preparation.

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ABSTRACT

Approximately 75% of Finland is covered by boreal forest. Intensive commercial forestry has shaped the Finnish landscape as well as the animal communities that inhabit it. It has been suggested that commercial forestry increases the density of voles in boreal ecosystems. Voles, especially those belonging to *Microtus*, are important prey items for many avian and mammalian predators and are susceptible to numerous pathogens, e.g., Puumala virus. Vole population densities can affect the prevalence of these diseases in the environment and, in some cases, pose a health risk to the local human population.

In this thesis, I studied the effects of a changing landscape on vole populations and the influence of dynamic vole population densities on other trophic levels in the ecosystem. The main questions in the thesis are: how is commercial forestry affecting small mammal populations?; how does habitat and the small mammal community influence the prevalence of Puumala virus?; what are the main factors regulating red fox (*Vulpes vulpes*) population density?; and what are the habitat preferences of red fox?

The effects of forestry on voles and Puumala virus were studied in northern Finland (Taivalkoski) between 2006 and 2010. Voles were trapped bi-annually in 40 separate forest locations using a small quadrat method. Bank voles (*Myodes glareolus*) were screened for Puumala virus antibodies in the laboratory. The factors regulating the red fox population were studied with long-term Finnish data sets for red fox, Eurasian lynx (*Lynx lynx*), hare (*Lepus spp.*), voles, and hunting bag. Red fox habitat preferences in relation to the Eurasian lynx were studied in southern Finland using data collected with GPS-collared foxes and lynx.

We found that the early stages of forest succession are preferred by *Microtus* and, thus, commercial forestry is increasing the amount of habitat used by *Microtus* voles. In the Finnish forest landscape, Puumala virus is found in forests of all ages as is its main host, the bank vole. However, the highest bank vole densities are found in mature forests. We also found evidence of a dilution effect in that the incidence of Puumala virus antibodies in breeding bank voles was lower when the abundance of other small mammal species was high.

Our results suggest that the red fox population is regulated by its main predator, the Eurasian lynx, in addition to its own abundance in the environment. The red fox hunting bag was surprisingly related positively to the red fox population growth. We also found a negative relationship between autumn vole density and fox population growth in the next year. We suggest that the red fox population is affected by both top-down and bottom-up factors.

We also found that red foxes favour agricultural areas, and that home range size is smaller in regions dominated by crop fields. Within the home range, foxes prefer open forests that have been recently clear-cut and replanted, where *Microtus* voles can be found more abundantly. In comparison to lynx, foxes tend to range within more modified habitats, e.g., agricultural and urban areas, where predator densities are lower and alternative resources can be found.

Commercial forestry is affecting vole population density and other trophic levels in boreal forests. The increasing abundance of apex predators (e.g., lynx) is limiting the density of the vole predators (e.g., red fox) and thereby driving the system and its trophic interactions in a new level.

TIIVISTELMÄ

Noin kolme neljäsosaa Suomen pinta-alasta on metsää. Metsätalous on kuitenkin vaikuttanut voimakkaasti suomalaisiin metsiin ja niiden eliöstöön. On esimerkiksi esitetty, että metsänhoito lisää myyrätiheyksiä. Myyrillä taas on tärkeä merkitys pohjoisten havumetsien ekosysteemissä. Myyrät, erityisesti peltomyyrän sukuiset myyrät (*Microtus*), ovat tärkeää ravintoa monille pedoille. Myyrissä myös esiintyy monia taudinaiheuttajia kuten Puumala-virusta.

Tutkin väitöskirjassani metsätaloussympäristön muutosten vaikutusta myyräpopulaatioihin ja edelleen myyräkantojen muutosten vaikutusta muihin lajeihin. Väitöskirjani tärkeimmät tutkimuskysymykset ovat: miten nykyaikainen metsätalous vaikuttaa pikkunisäkkäisiin, miten elinympäristö ja pikkunisäkäsyhteisön rakenne vaikuttavat Puumala-viruksen esiintyvyyteen, mitkä tekijät säätelevät kettukantaa ja minkälaista elinympäristöä ketut suosivat.

Metsätalouden vaikutuksia myyriin ja Puumala-virukseen tutkittiin pyytämällä myyriä Taivalkoskella vuosina 2006–2010. Metsämyyristä tutkittiin laboratorioissa Puumala-viruksen vasta-aineet. Kettukannan kokoon vaikuttavia tekijöitä tutkittiin hyödyntäen riistakolmiolaskentojen tietoja sekä saalistilastoja. Kettujen elinympäristön valintaa selvitettiin seuraamalla GPS-pannoitettujen kettujen liikkeitä Hämeessä.

Myyrätutkimuksissamme selvisi, että metsissä peltomyyriä esiintyy lähinnä hakkuualoilla ja taimikoissa. Metsätalous siis lisää peltomyyrille sopivia ympäristöjä metsissämme. Metsämyyriä ja siten myös lajin kantamaa Puumala-virusta esiintyy kaikenikäisissä metsissä. Metsämyyrätiheydet ovat kuitenkin keskimäärin korkeimpia vanhoissa metsissä. Löysimme myös tukea havainnolle, että pikkunisäkäslajien monimuotoisuus vähentää taudinaiheuttajan, esimerkiksi Puumala-viruksen, esiintyvyyttä alueella.

Tulostemme perusteella kettukantaan vaikuttavat pedot, saaliin määrä ja kannan tiheys. Ilvesten määrä ja kettukannan oma tiheys vaikuttavat negatiivisesti kettukannan kasvuun. Myös syksyinen myyrätiheys vaikuttaa negatiivisesti seuraavan vuoden kettukannan kehitykseen. Tiheää myyräkantaa seuraa usein romahdus, minkä seurauksena pedoilla on niukasti ravintoa saatavilla.

Havaitsimme, että kettujen elinpiirit ovat pienempiä maatalousvaltaisilla alueilla. Elinpiirilään ketut viettävät aikaa avoimissa metsissä, jotka ovat esimerkiksi hakkuualoja ja taimikoita. Näillä alueilla esiintyy myös peltomyyriä, jotka ovat tärkeää saalista. Kettujen tärkeimpään petoon, ilvekseen, verrattuna ketut suosivat enemmän maatalousalueita ja ihmisen asuttamia alueita, joilla riski joutua pedon saaliiksi on pienempi ja joilla on saatavissa ihmisten tarjoama ravintoa.

Väitöskirjatyöni tulokset osoittavat, että metsätalous vaikuttaa myyräpopulaatioihin ja myyrissä esiintyvän viruksen esiintyvyyteen. Myyräpetojen kantoihin vaikuttavat kuitenkin myös muut tekijät, esimerkiksi ilveskannan kasvu, joka rajoittaa kettukannan kokoa.

Summary

1. INTRODUCTION

1.1. Forestry and voles

Approximately three-quarters of Finland is covered by boreal forests (Ahti *et al.* 1968, Peltola 2014, Fig. 1) dominated by Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*). In the past, fire has played an important role in their natural disturbance and regeneration (Esseen *et al.* 1992, 1997; Angelstam 1996). As a consequence of modern management practices and control measures, large forest fires are now a rare occurrence and commercial forestry has replaced them as the main factor shaping the boreal forest landscape in Fennoscandia and North America (Loope 1991, Esseen *et al.* 1997, Peltola 2014).

Clear-cutting and the cultivation of forest plantations (i.e., a single age class) in Fennoscandia began during the 1940s (Esseen *et al.* 1992). Prior to this period, foresters relied on natural regeneration and selectively cut trees of a minimum diameter (Leikola 1984), which maintained a more natural age structure in Finnish commercial forests. In 2004, 81% of commercial forests were clear-cut and replanted with nursery seedlings (Peltola 2014). Swedish forests use similar techniques to their counterparts in Finland, and operate plantation cycles from 80 years in the south to 120–130 years in the north (Esseen *et al.* 1997, Äijälä *et al.* 2014). Although the commercial forest area in Finland has not changed significantly during the last 100–125 years, the area occupied by old natural forests has reduced and become more fragmented (Kouki *et al.* 2001). In last 50 years, the area of old-growth forest has decreased dramatically, especially in northern Finland, and 16% of the Finnish forest area is less than 20 years old (Peltola 2014). After clear-cutting, the light, humidity and nutrient conditions shift and induce changes in the vegetation, e.g., grasses and herbs flourish while mosses and dwarf shrubs suffer (Zobel *et al.* 1993, Hannerz & Hånell 1997, Pykälä 2004, Uotila & Kouki 2005).

Fennoscandia contains three species of *Myodes* voles (bank vole [*My. glareolus*], red vole [*My. rutilus*], grey-sided vole [*My. rufocanus*]) and four species of *Microtus* voles (field vole [*Mi. agrestis*], root/tundra vole [*Mi. oeconomus*], sibling vole [*Mi. epiroticus*] and common vole [*Mi. arvalis*]), with diversity being higher in the north (Henttonen & Hansson 1984). The two most abundant and widespread Fennoscandian species are the bank vole and the field vole. Old forests are the core habitat for the bank vole but especially during high population densities they can be found elsewhere (Hansson 1999,

Sundell *et al.* 2012, I). The core habitats for the field vole are fields, meadows and grassy mires but they also use recently clear-cut and open forests (Henttonen 1989, Sundell *et al.* 2012). Due to their different habitat requirements, commercial forestry affects different vole species in different ways. It is generally understood that the abundance of folivorous *Microtus* voles increases after clear-cutting (Hansson 1978, Henttonen 1989, Bogdziewicz & Zwolak 2014) while granivorous-folivorous *Myodes* species decline (Hansson 1978, 1999, Ecke 2002). However, in their meta-analysis of a European dataset, Bogdziewicz & Zwolak (2014) did not find a negative effect of clear-cutting on bank voles.

1.2. Voles as prey

Microtus and *Myodes* voles differ in their spacing behaviour. Breeding *Microtus* have small home ranges that can overlap (Myllymäki 1977, cf. Erlinge *et al.* 1990), while breeding female *Myodes* have larger territories (reviewed by Viitala & Hoffmeyer 1985, Viitala 1987). Due to these differences in behaviour, *Microtus* voles can reach 5–10-fold higher densities than *Myodes* species (Myllymäki 1977, Henttonen 1987).

Voles, and especially *Microtus*, are important prey items for many avian and mammalian predators such as the least weasel (*Mustela nivalis*), stoat (*Mustela erminea*), pine marten (*Martes martes*), common kestrel (*Falco tinnunculus*), short-eared owl (*Asio flammeus*), long-eared owl (*Asio otus*), Tengmalm's owl (*Aegolius funereus*) (Korpimäki 1986, Korpimäki & Norrdahl 1991a, Korpimäki 1992, Reif *et al.* 2001, Korpimäki & Hakkarainen 2012). Least weasels are vole specialists and *Microtus* are an essential food source (Korpimäki *et al.* 1991) during winter and the breeding season (Henttonen 1987). Red fox (*Vulpes vulpes*) is a common, mid-sized generalist predator (a so-called *mesopredator*) in Fennoscandia, where small mammals and especially *Microtus* voles comprise the main prey items in northern areas (Lindström 1989, Vainio *et al.* 1997, Kauhala *et al.* 1998, Dell'Arte *et al.* 2007).

1.3. Population fluctuations of voles and their predators

An important characteristic of the northern terrestrial environments is the low diversity of vertebrate guilds. This ecological simplicity creates a decoupling of prey and predator population densities and thus pronounced fluctuations in their relative abundances. While vole population fluctuations are irregular in North America (Hansson & Henttonen 1985, Boutin *et al.* 1995), they occur on rather predictable 3–5-year cycles in Fennoscandia (Hansson & Henttonen 1985, Hanski *et al.* 1991, Sundell *et al.* 2004). At present, a universally-accepted explanation for the mechanism(s) creating the population cycles is lacking, but predation by specialist predators and a shortage of winter food are commonly suggested (Hanski *et al.* 1991, Korpimäki *et al.* 1991, Korpimäki & Krebs 1996,

Hanski *et al.* 2001, Huitu *et al.* 2003, Huitu *et al.* 2004). Predation by resident mammalian specialists intensifies the amplitude of vole population densities, while predation by generalists and nomadic (avian) predators dampen them (Andersson & Erlinge 1977, Korpimäki & Norrdahl 1991b, Hanski *et al.* 2001). Results of a recent modelling study (Korpela *et al.* 2014) suggest that the interactions between voles and small mustelids is an important factor in Fennoscandian population cycles, but this interaction is contingent upon and modified by climate.

It has been reported that the amplitude of multi-annual cycles has been reducing at several long-term monitoring locations in Europe since late 1980s (Henttonen 2000, Hörnfeldt 2004, Ims *et al.* 2008, Cornulier *et al.* 2013), and has been linked to climate change (Cornulier *et al.* 2013). Ecke *et al.* (2006, 2010) suggested that commercial forestry also represents an important factor in the local long-term decline of the grey-sided vole in forest plantations of Fennoscandia. An interesting feature is that in northern Fennoscandia dampened cycles have recently returned (Henttonen, Ecke, Hörnfeldt, pers. comm.). The model applied by Hanski & Henttonen (1996) suggested that such long-term changes in the amplitude and frequency of rodent population cycles are not unexpected in multispecies prey-predator assemblages.

Reflecting the dynamics of local vole abundances, predators and small game species have earlier followed 3- to 5-year population cycles in northern Fennoscandia (Angelstam *et al.* 1984, Hansson & Henttonen 1985, Hanski *et al.* 1991, Sundell *et al.* 2004). However, small game species have shown less clear 6- to 7-year cycles in southern and central Finland (Lindén 1988). Synchronous population fluctuations have been explained by the alternative prey hypothesis (Hagen 1952, Lack 1954, Angelstam *et al.* 1984, 1985) and by the shared predation hypothesis (Norrdahl & Korpimäki 2000). The latter suggests that predators kill prey unselectively and the predation pressure against each species is determined by the abundance of their predators. The alternative prey hypothesis posits that predators concentrate on the main prey species when their densities are high and then predation pressure against alternative prey species is reduced. When densities of the main prey species decline, predators shift to the alternative prey and their populations are suppressed. Eventually, the survival and reproduction of the predators decline (Angelstam *et al.* 1984, 1985). In Fennoscandia, *Microtus* voles are the main prey item for many predators while bank voles (*Myodes glareolus*) are the most important alternate (Korpimäki *et al.* 2005), along with the eggs and young of small game species such as grouse (Tetraonidae) and hare (*Lepus* spp.). Of the resident predators, the pine marten, stoat and especially the red fox appear to align with the alternative prey hypothesis (Korpimäki & Norrdahl 1997, Kurki 1997).

Henttonen (1989) hypothesized that the abundance of *Microtus* voles had increased in response to an increase in the area of open grasslands, afforested fields and ditched bogs

created by commercial forestry. More voles led to higher densities of red fox and other small- and medium-sized predators. During the crash phase of a *Microtus* population cycle, predators shift to small game species and this phenomenon might explain to the decline of forest grouse populations in Finland observed during the 20th century (Lindén & Rajala 1981; Kurki *et al.* 1997, 1998; Sirkiä *et al.* 2010).

1.4. Regulation of the red fox population

Populations of mesopredators can be regulated by prey abundance (bottom-up) or by apex predators (top-down) (Elmhagen & Rushton 2007, Pasanen-Mortensen *et al.* 2013). The red fox is a common generalist mesopredator in Finland, where population densities tend to follow vole cycles (Angelstam *et al.* 1985). Although the red fox population is widely believed to be regulated by the availability of food, social factors have been implicated in southern Sweden (Englund 1970) and reproductive output is known to be density dependent in other canids (Sparkman *et al.* 2011). The main natural enemies of red foxes are large mammalian predators (Andersone & Ozolins 2004, Valdmann *et al.* 2005, Heldin *et al.* 2006), especially the Eurasian lynx (*Lynx lynx*) (Sunde *et al.* 1999, Andersone & Ozolins 2004, Heldin *et al.* 2006). The lynx population has increased dramatically in the last 20 years and the 2015 minimum population estimate for Finland is 2700–2800 adults (http://www.rktl.fi/riista/suurpedot/ilves/ilveksen_kanta_arviot.html, 9.10.2014), and the notion that lynx can suppress red fox populations has been suggested (Ludwig 2007, Elmhagen *et al.* 2010, Pasanen-Mortensen *et al.* 2013).

A loss of apex predators can permit a rise in the density of mesopredators that, in turn, suppresses the abundance of small prey species (*mesopredator release*; Soulé *et al.* 1988, Crooks and Soulé 1999, Ritchie & Johnson 2009). Conversely, an increase in apex predators can reverse the effects of a mesopredator. For example, the presence of dingoes (*Canis lupus dingo*) in Australia has been reported to suppress the abundance of introduced red foxes and facilitate a rebound of native marsupial numbers (Johnson *et al.* 2007, Southgate *et al.* 2007, Wallach *et al.* 2010, Gordon *et al.* 2015). Apex predators are affecting mesopredator survival and reproduction by both by consuming them and restricting their habitat use and behaviour (reviewed by Ritchie and Johnson 2009). The presence of top predators can also create a so-called “landscape of fear” for mesopredators (Laundre *et al.* 2001).

Red fox and lynx are both preying on game species (e.g., hares) in Finland (Pulliainen *et al.* 1995, Vainio *et al.* 1997, Kauhala *et al.* 1998, Dell’Arte 2007). Elmhagen *et al.* (2010) suggested that in eastern Finland lynx are suppressing red fox densities and that this has released the local mountain hare (*Lepus timidus*) population from top-down regulation, thereby facilitating a higher density. Hares are the main prey item for lynx but surveys

indicate that red foxes outnumber lynx 40:1, which explains the strongly negative effect of foxes on the hare population. Several studies have also emphasised the importance of fox predation on grouse (Marcström *et al.* 1988, Kurki *et al.* 1997, Kauhala *et al.* 2000). Culling the red fox population through hunting is considered to be an important technique in the management and health of game species.

1.5. Puumala virus

Small rodents harbour numerous pathogens and parasites. Several vole-borne pathogens can also infect humans, i.e., are zoonotic. Rodent-borne hantaviruses (family *Bunyaviridae*) cause hemorrhagic fever with renal syndrome and hantavirus cardiopulmonary syndrome in humans (Jonsson *et al.* 2010, Vaheri *et al.* 2013a, 2013b).

Human-mediated environmental disturbance (e.g. commercial forestry) can affect infection dynamics of pathogens by altering host population density or by influencing species richness and therefore intraspecific contact rate and transmission of the pathogen. The so-called “dilution effect” is a phenomenon where high species richness is associated with a decrease in the prevalence of one or more pathogens (Keesing *et al.* 2006, Dearing & Disney 2010, Keesing *et al.* 2010). Fennoscandian small mammal diversity is often higher in early succession stages of boreal forests inhabited by both *Myodes* and *Microtus* voles (I, II, Henttonen & Hansson 1984).

The most common hantaviral disease in Europe is nephropathia epidemica, a mild form of hemorrhagic fever with renal syndrome (Heyman *et al.* 2008, Vaheri *et al.* 2013a). It is caused by the Puumala virus (Brummer-Korvenkontio *et al.* 1980, Vapalahti *et al.* 2003) hosted by the bank vole. In the vole host, Puumala virus is persistent (Meyer & Schmaljohn 2000) and does not cause visible symptoms (Gavrilovskaya 1990, Bernshtein 1999, Meyer & Schmaljohn 2000) although it can reduce the winter survival of infected bank voles (Kallio *et al.* 2007). Transmission in the host is horizontal and occurs directly via aerosol excretions (Gavrilovskaya 1990, Kallio *et al.* 2006a). Epidemic peaks of human nephropathia epidemica follow the seasonal and multi-annual dynamics of bank vole abundance (Brummer-Korvenkontio 1982, Niklasson *et al.* 1995, Kallio *et al.* 2009). While the virus and its host are found in most European countries, most of the human infections occur in the boreal zone of northern Europe (Heyman *et al.* 2008, Vaheri *et al.* 2013a).

2. AIMS

Commercial forestry is drastically affecting the boreal ecosystem. The aim of this thesis is to understand the effects of a changing landscape on vole populations and, in turn, the influence of dynamic vole populations on other trophic levels. It has been argued that an increase in the number of *Microtus* voles has led to higher predator densities, and that this had a negative effect on the abundance of game species. Culling of predators has been seen as an important step in game management, and the aggregation of voles in certain habitats can affect the distribution of predators in the landscape. However, the habitat use and population density of mesopredators is also affected by the presence of apex predators. Changes in the landscape and small mammal community might also affect the prevalence of vole-borne pathogens, some of which can infect humans.

The main questions in this thesis are:

- How is commercial forestry affecting small mammal populations? (I)
- How does habitat and the small mammal community influence the prevalence of Puumala virus? (II)
- What are the main factors regulating red fox (*Vulpes vulpes*) population density: prey abundance, apex predators or hunting? (III)
- What are the habitat preferences of the red fox? Can the distribution of red fox prey or predators explain these preferences? (IV)

3. MATERIAL AND METHODS

3.1. Materials

All studies took place in the Finnish boreal zone. Fieldwork for studies I and II was conducted in the municipalities of Taivalkoski and Pudasjärvi in northern Finland (65° N, 28° E; Fig. 1), respectively. The study areas are located at the interface of the northern and central boreal zones (Ahti *et al.* 1968), where the mean monthly temperature at the closest weather station ranges from -12.8 °C in January to 14.6 °C in July. Bi-annual surveys of the vole community were made 2006–2010 (study I) and 2007–2010 (study II). The voles were snap-trapped in June and September at 40 forest stands using the small quadrat method (Myllymäki 1971). Stands represented four age classes: managed forests established (1) 3–8, (2) 9–15 and (3) 24–30 years after clear-cutting, and (4) unmanaged forests older than 100 years (Fig. 2). After trapping animals were flash frozen at -20 °C prior to dissection in the laboratory. The species, sex, weight, age and functional group were determined for each individual and the hearts of bank voles were preserved in phosphate-buffered saline for serological analyses. An estimate of vole density was made in the form of a trapping index, i.e., the number of animals trapped per 100 trap nights.

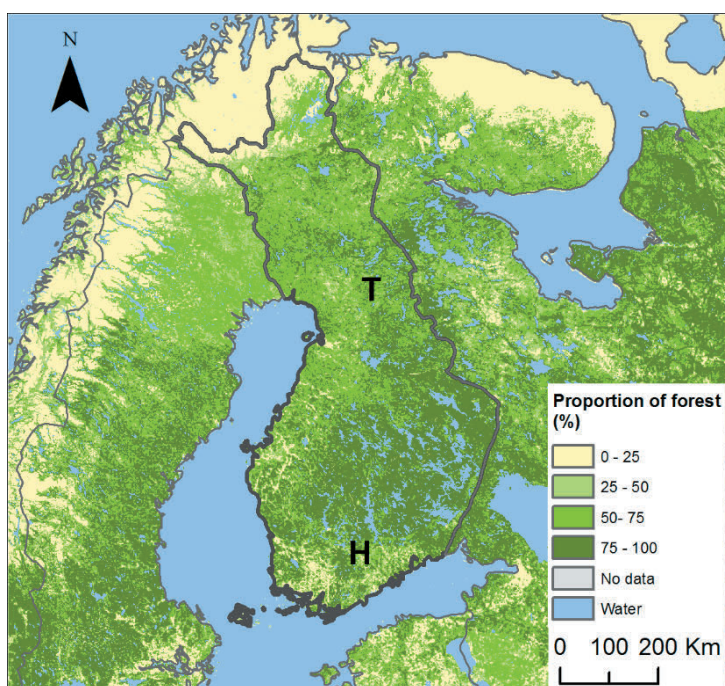


Figure 1. Locations of Taivalkoski (T) and Häme (H) study areas and proportion of forest cover in Finland.

In study II, bank voles were examined in the laboratory using an immunofluorescent antibody test to detect antibodies specific to the Puumala virus (Kallio-Kokko *et al.* 2006). Given that Puumala virus causes a chronic infection in bank voles (Meyer & Schmaljohn 2000), the presence of antibodies indicates infection. However, infected mothers can transfer antibodies to their offspring during gestation and lactation (Dohmae *et al.* 1993, Kallio *et al.* 2006b). Therefore, a statistical model incorporating the probability of being antibody positive in relation to body mass was used to distinguish individuals carrying maternal antibodies from those with antibodies generated in response to an infection.

Data for study III were gathered from the long-term monitoring projects of the (former) Finnish Game and Fisheries Research Institute and Finnish Forest Research institute (now the Natural Resources Institute Finland). Density indices of the red fox, Eurasian lynx and hare were based on Finnish wildlife triangle snow track counts covering the entire country (Lindén *et al.* 1996). We also used Finnish hunting bag statistics and data from nationwide vole censuses (Korpela *et al.* 2013, 2014). The rate of red fox population growth [calculated as $\ln(\text{fox density index in year } t+1 / \text{fox density index in year } t)$] was used as the response variable in statistical analyses.

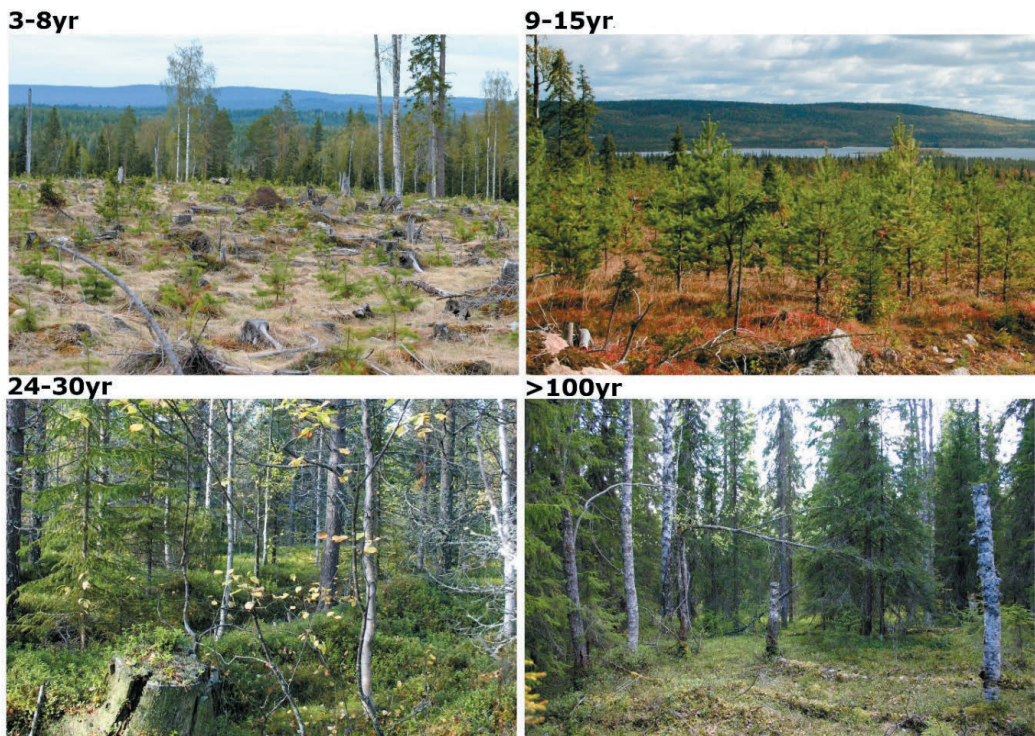


Figure 2. Forest age classes in 2006 in which the small mammal trappings for study I and II were performed.

In study IV, GPS-tracking of red fox and lynx was conducted in the southern boreal zone (~61°N, ~25°E) at Häme (Fig. 1) during 2011–2014. The mean annual temperature in the study area is 4.2 °C (from -6.5 °C in January to 16.6 °C in July). Snow cover lasts for approximately six months. In total, four male and three female red foxes were live-trapped by local hunters and fitted with GPS transmitters. The collars provided the position of each fox every four hours using GPS satellites, and an activity value every five minutes. Foxes were tracked for 28–216 days. The activity patterns and habitat preferences of red foxes were compared with that of 11 Eurasian lynx fitted with GPS collars in the same area.

3.2. GIS

Geographic information system (GIS) methods were used in studies III and IV. In III, spatial interpolation of local vole censuses was used to estimate the phase of the vole population cycle for the whole of Finland. In IV, the fox and lynx tracking locations were used to estimate the home range and activity of each animal. These values were then compared with the Corine land-cover dataset to reveal the habitat use of these species in the study area. For the red fox, minimum convex polygon (MCP), kernel 95% (K95), kernel 75% (K75) and kernel 50% (K50) home range estimates were calculated. For MCP, home range is estimated by drawing the smallest possible convex polygon that includes all known locations of the animal. It is the oldest and most commonly used home range estimation method (Powell 2000). The kernel method was used to estimate the utilisation distribution for each animal. This relies on a bivariate function giving the probability density that an individual is found at a certain point. The home range is the minimum area in which the individual can be found with certain probability (Worton 1995). The K95 was used as an estimate of the entire home range of each animal, and the K75 and K50 as estimates of its core. GIS analyses were done using Esri ArcGIS 10.1 software and AdehabitatHR and AdehabitatLT (Calenge 2006) packages in R statistical software (R Core Team 2014).

3.3. Statistical analyses

Generalised linear mixed models (GLMM) were used in studies I, II and III. These statistical methods enable the detailed analysis and exploration of complicated datasets, (e.g., count and probability data). GLMMs also take into account issues of autocorrelation and pseudoreplication (Pinheiro & Bates 2000, Bolker *et al.* 2009, O'Hara 2009). In I, a generalized additive mixed model (GAMM; Zuur *et al.* 2009) was used to distinguish individuals with maternal antibodies from those with acquired infections. When necessary, we used an information theoretic (i.e., parsimony)

approach to select the most appropriate model (Burnham & Anderson 2000). In IV, habitat use of red fox and lynx was studied using compositional analysis (Aebischer *et al.* 1993). Most of the statistical analyses were performed with appropriate packages in R (R Core Team 2014).

4. RESULTS AND DISCUSSION

4.1. Effects of commercial forestry on voles and Puumala virus

Commercial forestry has increased the proportion of forest area in an early stage of succession. Our results show that field vole densities peak in clear-cut and newly replanted commercial forests (I). Our study began in an acyclical and low density period for *Microtus* voles that lasted from the early 1980s to 2009 in northern Finland (Henttonen *et al.* 1987, Henttonen 2000, Henttonen & Wallgren 2001, Heikki Henttonen personal communication). Thus, field voles did not reach the densities reported in earlier studies (Henttonen 1987, Henttonen 1989) and were generally lower than that of bank voles, especially during the first few years of the study.

Here, we show that bank voles inhabited forests in all stages of succession, but their numbers were always highest in mature forest except for 2006 when their density peaked in seedling forests that had been replanted 9–15 years earlier. During low density periods, bank voles were mainly trapped in mature forests, which is consistent with earlier studies that observed how mature forests are their preferred habitat (Henttonen *et al.* 1977, Hansson 1978, Hansson 1999, Sundell *et al.* 2012). Bank vole densities were higher in 3–15 year-old forests than in 24–30 year-old forests, where the total rodent abundance was also the lowest. Our results suggest that the highest prey densities for predators are found in old and young succession stages depending on year and season while the rodent density is lowest in forests of intermediate succession stage. The middle-aged forests often have a thick canopy which leads to more sparse ground vegetation than younger and older forest stages. Rodent density is more stable in old forests than in young patches, where *Microtus* species exhibit more pronounced population fluctuations than *Myodes* species. Furthermore, young forests are mainly inhabited by *Myodes* species during high density periods.

Bank voles harbour the Puumala virus (Vaheri *et al.* 2013) and thus their distribution and abundance affects its prevalence in the environment. We found that Puumala virus reflected the distribution of the bank vole generally, and could be found in all successional stages of commercial forest in Finland (II). However, the Puumala virus infection rate of bank voles peaked in mature forests, and bank vole population density was positively related to infection rate. However, when the population density was taken into account, younger forests had relatively higher infection rates. We also found evidence for a “dilution effect”, i.e., a phenomenon in which infection rate is negatively correlated with the density of other small mammals (Keesing *et al.* 2006, 2010). Breeding bank voles in June had lower Puumala seroprevalence when the density of other small mammals increased. In managed

forests of Fennoscandia, the diversity of small mammal communities is higher in younger successional stages inhabited by *Microtus* and *Myodes* species (I, II, Henttonen & Hansson 1984, Ecke *et al.* 2002). The wide co-distribution of bank voles and Puumala virus in boreal landscapes explains why most of the human infections of nephropathia epidemica occur in the boreal zone of northern Europe (Heyman *et al.* 2008, Vaheri *et al.* 2013).

4.2. Factors limiting the red fox population

Populations of mesopredators can be limited by either prey abundance (bottom-up), by apex predators and hunting (top-down) (Elmhagen & Rushton 2007, Pasanen-Mortensen 2013), or by reproductive inhibition dependent on their own local abundance (Englund 1970). The red fox is a common and widespread mesopredator of Finland. We found that the yearly red fox population growth rate was negatively affected by the density of lynx in the winter and *Microtus* voles in the preceding autumn (III). We suggest that the negative impact of *Microtus* voles in autumn is due to the following population crash and low vole numbers in next year. In earlier studies red fox population changes have been linked to the vole population fluctuations in central and northern Fennoscandia (Angelstam *et al.* 1985). Contrary to our hypotheses the fox population growth was positively associated to the red fox hunting bag. We hypothesise that this is due to the higher hunting yield during the high population growth, not due to the real positive effect of hunting. Our results also show that red fox population growth is inversely proportional to density, a phenomenon which may be due to social factors or intraspecific competition. Englund (1970) reported that red fox populations in southern Sweden are socially regulated while they are more strongly influenced by the availability of food in the north.

Our results suggests that while top predator is present red fox population growth is affected by both bottom-up and top-down forces and any single factor does not explain the changes in the populating growth comprehensively. Red fox is an opportunistic predator and thus its numbers are influenced by environmental productivity and complexity (Elmhagen & Rushton 2007, Elmhagen *et al.* 2010) and thereby the overall abundance of a diverse prey base. The “mesopredator release” hypothesis posits that the loss or removal of apex predators enables the rise of mesopredator densities and thereby suppresses the abundance of small prey species, and conversely the return of apex predators will suppress the mesopredator population and enable the small prey species to recover (Soulé *et al.* 1988, Crooks & Soulé 1999).

4.3. Habitat selection of red fox

In IV, fox MCP home ranges ranged from 13.1 to 132.8 km². The kernel 50% (K50) represents the core of the home range, and we recovered estimates from 1.3 to 15.3 km².

Both MCP and K50 estimates are larger than the home ranges estimated by earlier studies (e.g., Kauhala *et al.* 2006). This could partly be due to methodological differences (VHF in earlier studies instead of GPS) and/or the environmental productivity being lower in our study area than elsewhere.

The home ranges (MCP, K95) of the tracked foxes contained a higher proportion of field area than the study area did as a whole. The size of the red fox K75 core was negatively correlated with the proportion of fields in the home range, i.e., a home range consisting of mainly field habitat was proportionally smaller. The proportion of agricultural and urban infrastructure correlates with the overall productivity of the area. Fields and urban areas were used mainly at night, suggesting they are used as foraging and hunting habitats. Open areas are favoured by *Microtus* voles which are an important prey item for red fox (Lindström 1989, Kauhala *et al.* 1998, Dell'Arte *et al.* 2007). Foxes also spent more time in fields and urban areas than their most important predator, the lynx. As such, the apparent preference of the red fox for modified or artificial habitats could partly be due to a trade-off to reduce their own predation risk while maximizing their ability to find prey or other nutritional resources.

Within the home ranges, areas with sparse tree cover were favoured over other forest areas and other habitats. Open forests are those that have recently been clear-cut or replanted, and are where the highest densities of *Microtus* voles are frequently observed (I). The preference shown for this habitat by the red fox could be due to the high vole densities that occur in these settings. Thus, our results are consistent with the hypothesis that modern silvicultural practice is favouring the predator (Henttonen 1989). Moreover, seedling stands and young forests can provide dense daytime shelter for foxes, and areas with sparse amounts of tree cover were used more during the day than at night.

5. CONCLUSIONS

Finnish forests, and the animal communities they support, are now profoundly affected by anthropogenic activity. Voles are one of the keystone species in boreal forests and changes in their abundance and distribution affect many species that depend on them as a food source. Commercial forestry increases the proportion of the forested landscape that is in an early stage of succession, i.e., ideal habitat for *Microtus* voles. Species richness of voles is higher in young forests inhabited by a mixed community of forest and grassland species. In Fennoscandia, Puumala virus and its principal host the bank vole are found in forests of all ages. However, bank vole densities are highest in mature forests, and host density is positively correlated with infection rate. We also observed a “dilution effect”, wherein breeding bank voles were less often infected by Puumala virus when the abundance of other small mammal species was higher.

The increased density of apex predator, the Eurasian lynx, has shifted the red fox population from one regulated by prey availability (i.e., bottom-up) to one regulated by also predation pressure (i.e., top-down) and with curtailed reproduction in response to its own population density. We suggest that greater numbers of lynx in the landscape will suppress red fox populations and induce a trophic cascade that benefits prey species such as hare and grouse. Since the start of the wildlife triangle scheme in 1989, the red fox indices have been stable or have slowly decreased in all game management districts of Finland.

In southern Finland, the red fox established home ranges in agricultural areas, and the size of a home range was negatively correlated with the proportion of the range that comprised field habitat, i.e., home ranges comprised mainly of fields were proportionally smaller. Within their home range, foxes prefer open forest areas such as those that had been recently clear-cut and replanted. This could be due to the high abundance of voles and the cover provided by these habitats. This finding supports the hypothesis that forestry is favouring the predators (Henttonen 1989). Foxes use agricultural and urban areas more than their most important predator, the lynx. This could be due to a predator-avoidance strategy, or due to the food and other resources those areas provide. Fields and urban locations are used by foxes relatively more during the night, suggesting they are important feeding grounds, but could also be influenced by the human activity during the day. It has been suggested that foxes are moving more closer to urban settlements than ever before and that this could be caused by the lynx. Unfortunately, data pertaining to habitat use by red foxes in Finland prior to the recovery of lynx are not available. The main species interactions studied in the thesis are presented in the figure 3.

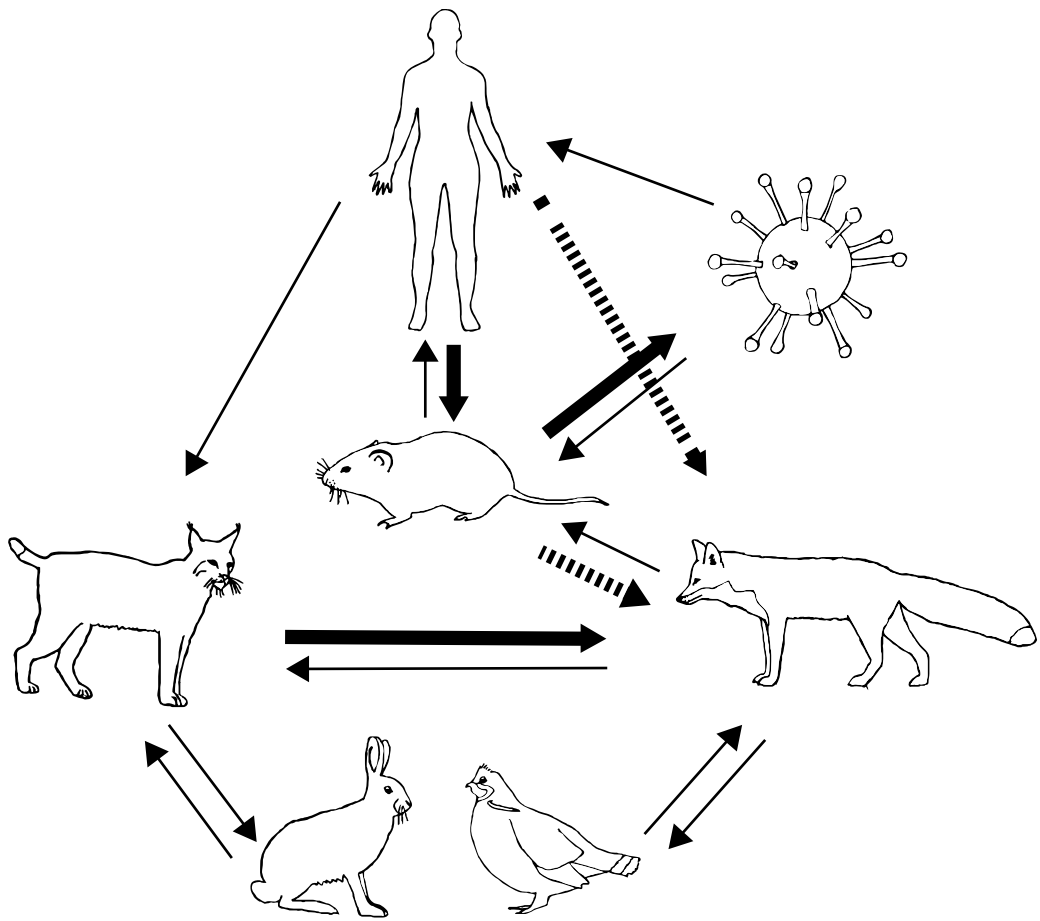


Figure 3. The main species interactions studied and discussed in this thesis. The thick black arrows represent the newly-discovered population-level interactions, the thick dashed arrows represent newly-discovered but controversial interactions and thin arrows represent other plausible interactions.

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