

Cyclic Voles and Puumala Hantavirus in a Changing Boreal Landscape

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Cover: Grey-sided vole (*Myodes rufocanus*) in a stone field habitat
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Abstract

Land-use change is causing extinction of species globally, while also increasing the risk of disease exposure to humans through augmented interactions with wildlife, when humans live and work in manipulated ecosystems or when animals seek shelter/refuge in man-made infrastructure.

Forestry is one such activity, which is continually altering forest structure worldwide, causing habitat loss for many specialized forest species. This study investigates the population ecology of three cyclic vole species, *Myodes rufocanus*, *Myodes glareolus* and *Microtus agrestis*, in relation to intensive forestry in northern Sweden. *M. glareolus* is also the natural reservoir of Puumala hantavirus (PUUV) which is important from a public health perspective since PUUV causes nephropathia epidemica in humans. *M. rufocanus* and *M. agrestis* declined substantially in density and distribution during the 1970-80s while *M. glareolus* only marginally declined and is still the most common species in the region.

The decline of *M. rufocanus* was related to habitat loss. The cumulated impact from long-term clear-cutting explained local extinctions of *M. rufocanus*. The species is also dependent on maintained connectivity between old forest and shelter-providing stone fields. In contrast, local extinction of *M. agrestis* was not related to forestry, suggesting action of another strong driver. *M. agrestis* re-colonized most of the study area during 2010-2011, two years that were characterised by cold winters and a thick snow cover, suggesting a climatic driver in this case. Occurrence of PUUV infected *M. glareolus* was negatively related to the impact of long-term clear-cutting in the surrounding landscape. PUUV infected *M. glareolus* survived during low density periods of the vole cycle in old forests.

In summary, the main driver of the decline in density and distribution of *M. rufocanus* appeared to be intensive forestry. PUUV infection dynamics also appeared to be related to forestry. Since land-use changes and climate changes have coincided in Fennoscandian forests, I suggest that future studies should focus on estimating the relative impact of these two factors on pathogen and vole population dynamics.

Keywords: Boreal forest, Clear-cuts, Connectivity, Forestry, Habitat loss, *Myodes rufocanus*, *Myodes glareolus*, *Microtus agrestis*, Puumala Hantavirus, Spatiotemporal changes

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Dedication

To my family

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Ecke, F., Magnusson, M., Hörnfeldt, B. (2013). Spatiotemporal changes in the landscape structure of forests in northern Sweden. *Scandinavian Journal of Forest Research* 28, 651-667.
- II Magnusson, M., Bergsten, A., Ecke, F., Bodin, Ö., Bodin, L., Hörnfeldt, B. (2013). Predicting grey-sided vole occurrence in northern Sweden at multiple spatial scales. *Ecology and Evolution* 3, 4365-4376.
- III Magnusson, M., Ecke, F., Khalil, H., Olsson, G., Evander, M., Niklasson, B., Hörnfeldt, B. (submitted). Spatial and temporal variation of hantavirus infection in managed forest landscapes.
- IV Magnusson, M., Hörnfeldt, B., Ecke, F. (manuscript). Evidence for different drivers behind dampening of vole cycles across Europe.

Papers I and II are reproduced with the permission of the publishers.

The contribution of MM to the papers included in this thesis was as follows:

- I MM analyzed parts of the data and wrote the majority of the manuscript.
- II MM formulated the research questions, collected the species data, analyzed the data and wrote the majority of the manuscript.
- III MM formulated parts of the ideas and research questions, analyzed the majority of the data and wrote the majority of the manuscript.
- IV MM formulated the research questions, analyzed the data and wrote the majority of the manuscript.

1 Introduction

1.1 Land-use change in boreal forests

Intensive forestry is continually reshaping forests globally, leading to habitat loss and declines in specialized forest species (Lindenmayer & Franklin, 2002). Boreal forests have a long history of human impact, and traces of human activity can be found almost everywhere, even in natural forest reserves (Josefsson *et al.*, 2009). Selective logging affected almost all forested land in northern Sweden except mountain forests between 1850 and 1950 (Linder & Östlund, 1992; Kardell, 2004), while intensive clear-cutting practices began around the 1950s (Ebeling, 1959), with negative effects on many forest species (Andrén, 1994; Esseen *et al.*, 1997). In Sweden >2000 forest species are nationally red-listed (Gärdenfors, 2010), of which many are dependent on old forest structures such as coarse woody debris and old trees (Nilsson *et al.*, 2001). The land-use shift caused by clear-cutting is characterized by a change from old-growth forests with a multi-layered canopy and a large supply of dead wood to monocultures with a single-layered canopy and a shortage of dead wood (Esseen *et al.*, 1997; Östlund *et al.*, 1997). For boreal vole species, different forest age-classes are linked to structural habitat factors, such as dead wood, that affect vole density and distribution (Ecke *et al.*, 2002).

1.2 Cyclic voles

Voles are key prey species in boreal and arctic ecosystems for specialist predators such as mustelids (*Mustela* spp.) and Tengmalm's owl (*Aegolius funereus*). These predators show strong cyclic patterns in their population fluctuations, which appear to be dependent on vole cycles (Hörnfeldt, 1978; Henttonen, 1987; Hörnfeldt *et al.*, 1990; Hanski & Henttonen, 1996). Small mammal research has mainly focused on understanding the causes and consequences of the vole population cycles (see e.g. Krebs & Myers, 1974;

Hörnfeldt, 1994; Stenseth, 1999; Korpimäki *et al.*, 2002; Strann *et al.*, 2002), but other objectives also exist. For example, voles tend to be regarded as pest species in forest management (Larsson, 1975), cause crop damage on agricultural land in some parts of central Europe (Jacob *et al.*, 2013) and are vectors for many zoonotic diseases (Davis *et al.*, 2005; Kallio *et al.*, 2009; Olsson *et al.*, 2009; Tersago *et al.*, 2011). A few recent studies have focused on conservation issues and suggested that population declines in Europe are related to intensive forestry (Henttonen, 1998; Ecke *et al.*, 2006; 2010, Christensen *et al.*, 2008) or predation by invasive species such as the American mink (*Mustela vison*; Aars *et al.*, 2001). There is also a growing body of literature exploring the effects of a changing climate on vole and lemming population dynamics (Ims *et al.*, 2008; Kausrud *et al.*, 2008; Brommer *et al.*, 2010; Korpela *et al.*, 2013).

1.2.1 Distribution and habitat preference of voles in northern Sweden

In lowland forests of northern Sweden south of the Arctic Circle, the three most common vole species are the grey-sided vole (*Myodes rufocanus*) which is the focal species of this thesis, the bank vole (*Myodes glareolus*) and the field vole (*Microtus agrestis*). These three species make up >90 % of all small mammals (including shrews, voles, mice and lemmings) trapped in the ongoing National Environmental Monitoring Programme of small mammals (NEMP) in northern Sweden, set up in 1971 (Hörnfeldt, 2004). Grey-sided voles and bank voles are forest species (Siivonen, 1968), but may occur elsewhere in open habitats (Hansson, 1978). The field vole inhabits meadows, young forest plantations and forests with grasses in the field layer (Hansson, 1977). Field voles are considered superior to the grey-sided vole in competition for space (Viitala, 1977) but their habitats rarely overlap in boreal forests (Löfgren, 1995). The grey-sided vole is dominant over the bank vole in space use and female grey-sided voles may limit the breeding density of bank voles (Löfgren, 1995).

Habitat preferences for these species differ between various parts of their distribution range. The grey-sided vole occurs throughout large parts of northern Eurasia (Fig. 1; Kaneko *et al.*, 1998) in both lowland forests (Hörnfeldt, 1994; Löfgren, 1995) and in the arctic tundra (Grellman, 2002). On Hokkaido in Japan, the grey-sided vole prefers forest plantations (Saitoh *et al.*, 1998) but in lowland forests of northern Sweden, it is found mainly in old pine forests (Ecke *et al.*, 2006). The bank vole is a generalist species found in most forested areas throughout Europe (Siivonen, 1968). Their preferred habitat choice in northern, boreal Europe, especially during winter, is old, multi-layered coniferous forest (Ecke *et al.*, 2002). In regions of Europe with

temperate broad-leaved forest, bank vole dynamics are linked to years of high tree seed production (Tersago *et al.*, 2009) and their habitat preference is broad-leaved forest (Linard *et al.*, 2007b). Field voles occur in northern and central Europe and large parts of Russia (Siivonen, 1968) and their preferred habitat choice is mainly based upon availability of grasses and forbs (Hansson, 1977).

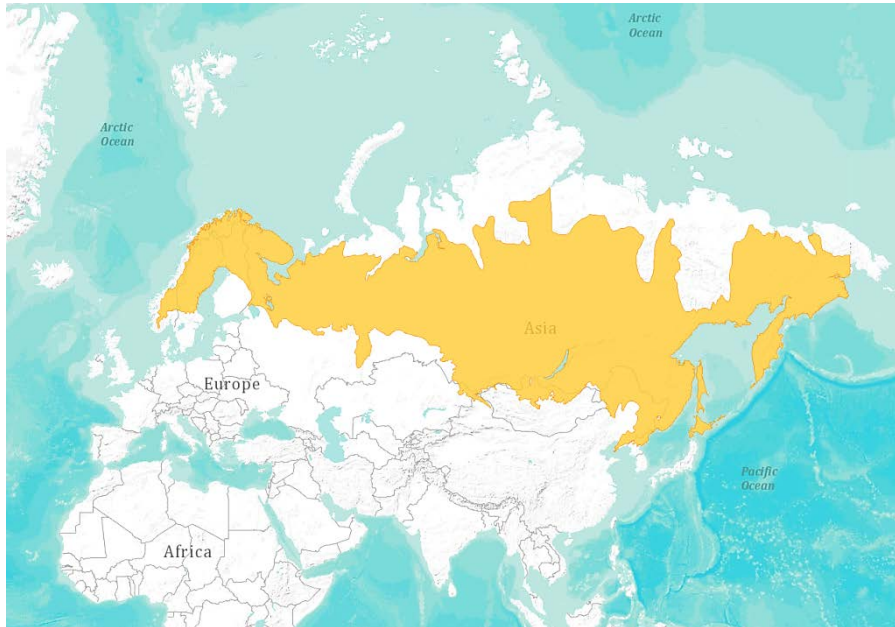


Figure 1. Distribution of the grey-sided vole (*Myodes rufocanus*) according to the International Union for Conservation of Nature (IUCN; Sheftel & Henttonen, 2008). Published with permission from IUCN.

1.3 Grey-sided vole decline and habitat loss

The grey-sided vole experienced a substantial decline in density and distribution in northern Sweden during the 1970s and 1980s (Fig. 2; Hörnfeldt 1994, 2004, 2014). Several studies have found negative effects of forest clear-cutting on grey-sided vole density and distribution (Ecke *et al.*, 2006, 2010; Hörnfeldt *et al.*, 2006; Christensen *et al.*, 2008). For long-term persistence of the grey-sided vole in northern Sweden it has been suggested that large patches of old pine forests are needed (Christensen *et al.*, 2008) and that habitat fragmentation in the surrounding landscape is kept below a certain threshold (Ecke *et al.*, 2006). However, no long-term studies of landscape changes in

relation to the grey-sided vole decline in northern Sweden have yet been presented. Grey-sided voles have also declined in other parts of their distribution range, such as in natural forests in Pallasjärvi, Finland (Henttonen, 2000), and the overall population trend is decreasing according to the IUCN Red List (Sheftel & Henttonen, 2008). It is possible that the overall decline is caused by a multitude of factors such as disease outbreaks, forestry induced landscape changes and climate changes, depending on sampling location.

It has been suggested that the overall dampening of vole cycles across Europe since the mid-1980s is driven by climate changes resulting in warmer winters (Cornulier *et al.*, 2013). Dampening of vole cycles is associated with a reduction in average population densities (Korpela *et al.*, 2013). Disease outbreaks may also affect vole populations but few studies have investigated how diseases affect the health and survival of voles (but see Kallio *et al.*, 2007). Recent evidence from Kielder Forest, northern England shows that viral pathogens (Cowpox virus) can regulate population cycles of field voles (Burthe *et al.*, 2008; Smith *et al.*, 2008). In addition, Kallio *et al.* (2007) showed that bank vole winter survival was hampered by Puumala hantavirus (PUUV; family *Bunyaviridae*; genus *Hantavirus*) infection. For the grey-sided vole, no studies have been carried out on the negative effects of disease to my knowledge.

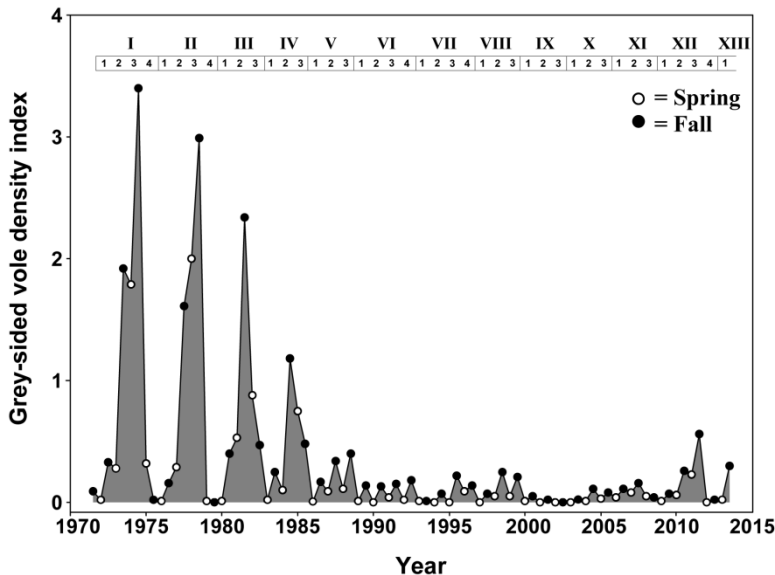


Figure 2. Density index (number of trapped individuals per 100 trap-nights) of grey-sided voles (*Myodes rufocanus*) in northern Sweden in spring (open circles) and fall (closed circles) 1971–2013 from fall 1971 ($n = 58$ sampling plots). Vole cycles numbered with roman numerals and each cycle covers three to four years. Figure from Paper IV.

1.4 Forestry effects on Puumala Hantavirus

Small mammals such as bats and rodents are reservoirs to many emerging infectious diseases, for example various hantaviruses (Yanagihara *et al.*, 1984; Childs *et al.*, 1994). Emerging zoonotic diseases are often thought to be transferred between animals and humans in boundaries between human settlements and natural habitats such as forests (Despommier *et al.*, 2007). Clear-cutting of forests has globally resulted in a landscape with “ecotones within ecotones” consisting of forest edge habitats at the local scale and fragmented forests at the landscape scale (Despommier *et al.*, 2007). In Fennoscandia, the bank vole carries PUUV causing nephropatia epidemica (NE) in humans (Brummer-Korvenkontio *et al.*, 1980; Yanagihara *et al.*, 1984). The density of PUUV infected voles are related to particular environmental characteristics associated with old growth moist forests (Olsson *et al.*, 2005), but infected animals can occur in all forest age-classes and sometimes with higher prevalence (proportion of PUUV infected voles) in younger forests (Voutilainen *et al.*, 2012). As previously mentioned, it has been shown that bank voles carrying PUUV have a lower winter survival (Kallio *et al.*, 2007). However, no study has yet investigated the influence of boreal forest landscape structure on occurrence, density and winter survival of PUUV infected voles. Landscape properties, such as large patches of broad-leaved forests are likely to increase the proportion of PUUV infected bank voles in temperate forest regions of Belgium (Linard *et al.*, 2007b) and increase PUUV infection risk for humans (Linard *et al.*, 2007a).

1.4.1 Environmental monitoring of zoonotic diseases

To understand spatial epidemiology, long-term data are needed on dynamics of virus prevalence in host species in relation to spatiotemporal changes in landscape properties (Ostfeld *et al.*, 2005). Both land-use changes (Suzan *et al.*, 2008) and climate changes (Shope, 1991) have proven to be drivers of change in virus prevalence in host populations. In USA and Canada, environmental monitoring programmes have collected data on prevalence of the Sin Nombre Hantavirus, which can be fatal to humans, in populations of the deer mouse (*Peromyscus maniculatus*; Mills *et al.*, 1999; Langlois *et al.*, 2001). Such long-term data on temporal dynamics of disease incidence is of great importance for human risk assessment (Dearing & Dizney, 2010; Mills *et al.*, 2010) and for understanding pathogen ecology (Carver *et al.*, 2010). There is a need for monitoring zoonotic diseases in natural host populations elsewhere in the world (Dearing & Dizney, 2010). Environmental monitoring of small mammals exists in northern Sweden (NEMP; Hörnfeldt, 1994, 2004, 2014) and Finland (Henttonen, 2000), but as yet no zoonotic disease

monitoring occurs. However, trapped animals from NEMP are stored deep-frozen in the Swedish Environmental Specimen Bank (Odsjö, 1997), providing an excellent opportunity for studying various zoonotic diseases transmitted by small mammals retrospectively.

1.4.2 Hantavirus prevalence in relation to rodent diversity

Declines in animal diversity globally due to, for example, forestry, have been suggested to impact emergence and transmission of infectious diseases (Keesing *et al.*, 2010; Suzan *et al.*, 2011). The main hypothesis, the so-called ‘dilution effect’, is that a more diverse animal community will increase the number of non-competent hosts and create fewer opportunities for individuals of the host species to contact with each other and transfer the pathogen (Keesing *et al.*, 2006). Effects from a less diverse animal community on pathogen prevalence in host populations have been shown in both experimental approaches (Suzan *et al.*, 2011) and through studying temporal changes in diversity (Carver *et al.*, 2011). However, the concept has also been criticized (Randolph & Dobson, 2012), which has led to a discussion about the generality and applicability of the concept (Ostfeld, 2013). Since the diversity of the small mammal community in northern Sweden has declined, especially due to declines in numbers of the grey-sided vole but also the field vole since the 1970s (Hörnfeldt, 1994; 2004; 2014), the long-term prevalence of PUUV in the bank vole population may also have been affected.

1.5 Spatiotemporal landscape changes

Recent developments in satellite imagery have the potential to improve our understanding of species-landscape interactions (Kerr & Ostrovsky, 2003; Turner *et al.*, 2003) and spatial epidemiology (Ostfeld *et al.*, 2005). However, the use of time-series of satellite imagery, aerial photographs or other geographical data in relation to spatiotemporal changes in species occurrences is a great challenge for spatial ecology (Gu *et al.*, 2002). Only a few studies exist (see e.g. Helle & Järvinen, 1986; Lindborg & Ericsson, 2004; Johansson *et al.*, 2008). Most studies are limited by either a lack of adequate knowledge on (1) species specific dispersal distances or/and home range size (Angelstam *et al.*, 2004), (2) historical occurrence and abundance of species (Kuussaari *et al.*, 2009) or (3) lack of data on spatiotemporal changes in landscape structure (Nagendra *et al.*, 2004).

2 Objectives

The aim of this thesis is twofold: (1) to study the decline of the grey-sided vole in particular, but also of the field vole, in relation to changes in forest landscape structure and, (2) to evaluate whether these landscape changes have also affected the distribution of PUUV and the density of PUUV infected bank voles.

This thesis has the following main objectives:

1. To study spatiotemporal changes in landscape structure caused by clear-cutting of old forests in northern Sweden.
2. To predict grey-sided vole occurrence in managed forest landscapes in northern Sweden at multiple spatial scales.
3. To investigate the distribution and density of PUUV infected bank voles in relation to habitat and landscape properties in managed forests.
4. To test whether there is a relationship between the long-term decline of the grey-sided vole and field vole population and landscape changes due to clear-cutting.

I will discuss the results in relation to (1) the climate change hypothesis as a common driver for the Europe-wide dampening of vole cycles and, (2) the effect of long-term land-use changes on the diversity of small mammals and dynamics of PUUV.

3 Material and methods

3.1 Study area and design

3.1.1 Papers I, III and IV

The study area for Papers I, III and IV was situated in the lowland boreal forests within the middle boreal region (Fig. 3; Ahti *et al.*, 1968). The vegetation type composition in the 100×100 km study area in 2000 was 53 % coniferous forest, 11% clear-cuts, 8 % young forest, 7 % mixed forest, 7% water, 7 % mires, 5 % agricultural land and 2 % deciduous forest (for definition of vegetation types see Swedish Land Survey, 2003). The study area constituted 16 regularly distributed 5×5 km areas. Each 5×5 km area consisted of four non-overlapping 2.5×2.5 km sub-areas with a 1-ha sampling plot in the centre of each. The vole sampling plots were represented by a 90 m trapping line with 10 trap stations centred along one of the diagonals. In total, out of 64 2.5×2.5 km potential sub-areas only 58 plots were trapped on, since some sampling plots were placed on unsuitable land cover types such as lakes. Voles have been monitored by snap-trapping twice a year since fall 1971, in spring and fall as part of the NEMP (Hörnfeldt, 1978, 1994, 2004, 2014). Permission to trap small mammals was obtained by the Swedish Environmental Protection Agency and from the Animal Ethics Committee in Umeå.

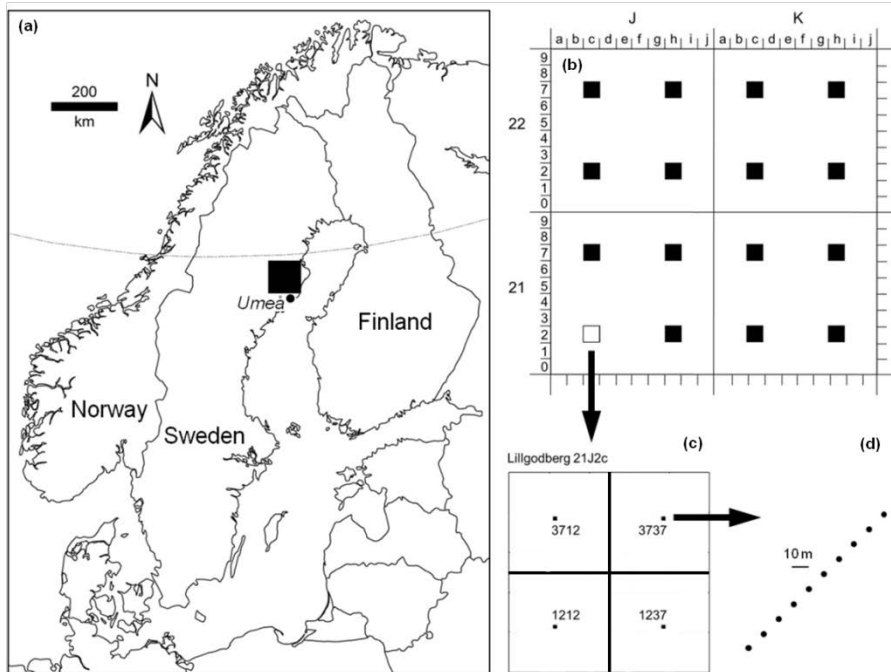


Figure 3. (a) Study area (black square) located in northern Sweden consisting of (b) 16 regularly distributed 5×5 km areas. (c) Each 5×5 km area contained four 1-ha sampling plots, each in the center of one of four 2.5×2.5 km sub-areas. Each sampling plot was represented by (d) a 90 m trapping line with 10 trap stations. Each of those trap-stations contained five snap-traps placed within a circle of a 1 m radius. In total, 58 out of 64 plots were sampled; six sampling plots fell on unsuitable land cover types such as water and were not trapped.

3.1.2 Paper II

The study areas for Paper II were situated in two old pine dominated landscapes in the interior of Västerbotten county and towards the coast in the eastern part of Norrbotten county, northern Sweden (Fig. 4). In Västerbotten, 23 sampling plots were surveyed in fall 2010 and 2011 (I in Fig. 4) and in Norrbotten, 16 plots in fall 2010 (II in Fig. 4). Each sampling plot, representing a 1-ha square, was randomly placed within a patch of old forest and consisted of a 90 m long trapping line with 10 trap stations centred along one of the diagonals. The trapping method was the same as the one used in Papers I, III and IV to facilitate comparisons of vole densities (no. of voles / 100 trap nights).

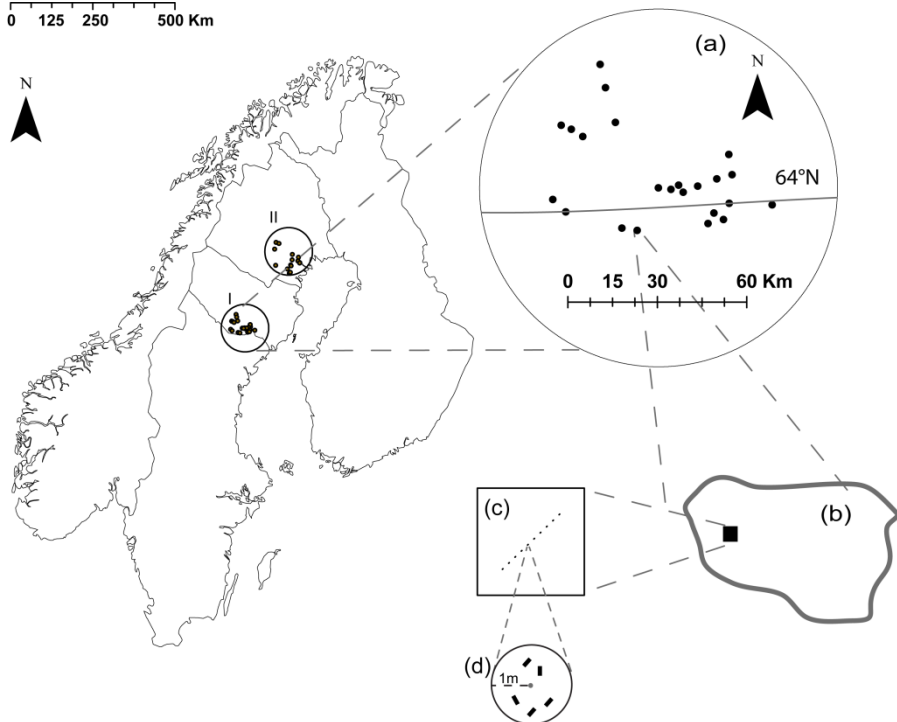


Figure 4. Study areas (circles) located in Västerbotten (I) and Norrbotten (II) county, northern Sweden. In Västerbotten, 23 sampling plots were surveyed (a) and in Norrbotten 16 plots. Each plot representing a 1-ha square was randomly placed within a patch of old forest >60 years (b). The surveyed line transect (representing the sampling plot) consisted of 10 trap stations along a diagonal (c) with five snap traps placed within a circle with a 1m radius at each trap station (d).

3.2 Vole, habitat and landscape data

3.2.1 Paper I

To produce a time-series of land-use changes due to clear-cutting in the study area (Fig. 3), vegetation maps produced by the Swedish Land Survey from 1980 were initially used as a reference. These maps were derived from interpreting infrared aerial photographs (Andersson, 2009) of the 16 regularly distributed 5×5 km areas within the study area (Fig. 3). The change in cover of four forest vegetation types (lichen, mesic, moist and wet) due to clear-cutting was updated backwards and forwards in time from 1980 using corresponding aerial black-and-white photos from 1954 to 2005. The forest types correspond to the moisture gradient from very dry to wet applied in the north Swedish forest type scheme (Arnborg, 1990). For the early period, photos were available from 1954 and 1964 and for the time period 1970-2005, with a 4-5

year interval. Changes in landscape structure from 1954 to 2005 were analysed with the FRAGSTATS 3.3 software (McGarigal & Marks, 1995) focussing on ecologically important landscape metrics such as mean patch size of old forest (ha; Ecke *et al.*, 2006), forest fragmentation index (%; Fahrig, 2003) and proportion of old forest in the landscape (%). The study area was divided into an inland (J in Fig. 3) and coastal region (K in Fig. 3) based on different timing of forest landscape changes.

In a global biodiversity meeting in Nagoya, Japan 2010 (COP 10), the participating countries agreed that at least 17 % of all terrestrial areas on a global basis should be conserved through ecologically representative and well-connected systems of protected areas (Convention on Biological Diversity, 2010). As such, a gap-analysis was used with a similar approach as used by Angelstam *et al.* (2010). The year 1954 was set as the base year and 2005 as the end year. The deficit in protected forest area in 2005 to fulfil the 17 % protection goal was calculated for each of the four forest types.

The expression *cut-over forest* is used throughout this thesis. Cut-over forest is defined as a forest plantation that has been clear-cut sometime in the past but not necessarily during the last 0-10 years, which is the normal definition of an open clear-cut. Data on changes of the amount of cut-over forest in the landscape surrounding each sampling plot presented in Paper I was later used in Papers III and IV in relation to changes in vole density and distribution. Old forest was in Papers I, III and IV defined as never clear-cut, multi-layered forest and the dominating age-class was approximately 81-120 years according to the Swedish National Forest Inventory (2014). In Paper II, old forest was defined as forest >60 years.

3.2.2 Paper II

To predict grey-sided vole occurrence at multiple spatial scales in lowland forests in northern Sweden, outside the NEMP, information on habitat and landscape requirements from previous studies (Christensen & Hörnfeldt, 2006; Ecke *et al.*, 2006; 2010, Hörnfeldt *et al.*, 2006, Christensen *et al.*, 2008) was used. Initially, two regions in northern Sweden with pronounced amounts of old pine forest were selected (Fig. 4). Within those landscapes all patches of forest >60 years old were mapped, and size and connectivity indices were calculated for each patch (IIC; Pascual-Hortal & Saura, 2006). Since Christensen *et al.*, (2008) proposed that future studies of occurrence and density of grey-sided voles ought to be carried out in pristine areas, a range of small to large patches, preferably within protected areas (range: 2.6 - 2370 ha), were selected. These patches were roughly categorized based on their area (small, large) and isolation (low, high connectivity). The aim was to get the

most extreme combinations of large and small patches with high or low isolation.

In addition, a detailed microhabitat survey of biotic and abiotic variables was carried out at each trap-station. At the landscape scale, geological data was obtained from the Swedish Geological Survey (Stendahl *et al.*, 2009), in order to map size and location of stone fields. Only stone field clusters >100 ha with an inter-distance of max 1000 m between individual stone fields were considered in the analyses.

3.2.3 Paper III

To study bank vole and PUUV infected bank vole dynamics in relation to forestry, bank vole data from 1979-1986 from the NEMP were used, representing different phases/years of two successive vole cycles, I: 1979-82 and II: 1983-85 and the first year of a third cycle (III: 1986). Voles were screened for antibodies to PUUV (see Niklasson *et al.*, 1995), and 422 voles were found to be positive (17 % of the total number of voles). Bank voles carrying antibodies were termed PUUV infected since PUUV causes a life-long persistent infection in bank voles (Meyer & Schmaljohn, 2000). As has been pointed out in recent years, young voles can carry maternal antibodies to PUUV, postponing PUUV infection (Kallio *et al.*, 2006). Consequently, following Voutilainen *et al.*, (2012), all voles <14.4 g were treated as not being infected ($n = 46$).

To explain density and distribution of non-infected and PUUV infected bank voles by habitat and landscape properties, data from Paper I for each 2.5×2.5 km sub-landscape ($n = 58$; Fig. 3c) were used. At the local scale, habitats were characterised broadly into categories by the dominant habitat type along the trapping line. Four habitat types were used; (1) cut-over forest ($n = 15-19$ plots), (2) old forest ($n = 28-32$ plots), (3) mires ($n = 9$ plots) and (4) meadows ($n = 2$ plots). Note that four old forests were clear-cut during the study period so the sample sizes for cut-over and old forest changed over time. At the landscape scale, two landscape metrics were used: focal patch size of old forest (ha; i.e. the forest patch surrounding the sampling plot) and proportion of cut-over forest (%).

3.2.4 Paper IV

To investigate whether altered forest structure due to forestry practices was related to the local extinction of the grey-sided vole and the field vole in the study area, vole data from the NEMP in 1971-2013 were used, representing different phases/years of twelve successive vole cycles (1972-2012). Subsequent cycles were numbered with Roman numerals (I-XII) and each

cycle covered three to four years (for detailed definition of vole cycles, see Hörnfeldt, 1994, 2004). In fall 2011, grey-sided voles were also trapped in 13 stone fields derived from geological maps (Stendahl *et al.*, 2009) adjacent to the permanent sampling plots in the western part of the NEMP study area.

At the habitat scale, similar habitat type categories as in Paper III (cut-over forest, old forest and mires) were related to density of grey-sided voles in spring and fall, 1971-2013. To define the habitat types, a combination of (1) forest data from Paper I, (2) field protocols from the NEMP and (3) manual field controls in 2012-2013 were used.

At the landscape scale, data of forest landscape structure changes from Paper I was available from 1970-2005, corresponding to cycle I-XI (1972-2008). The paper focussed entirely on spatiotemporal changes in the proportion of cut-over forests in each 2.5×2.5 km sub-area ($n = 58$), linked to presence/absence of the grey-sided vole and the field vole and density of the grey-sided vole. In addition, size and quality of all stone fields within 500 m from the 58 sampling plots were surveyed, and we investigated whether the connectivity between sampling plots and stone fields had been broken by clear-cutting in 1970-2005.

In the final analysis on changes in grey-sided vole density, both forest landscape data and stone field data were used, and the 58 sampling plots were classified into four different landscape settings: (1) connected to stone fields and <20 % cut-over forest in the surrounding landscape, (2) connected to stone fields and >20% cut-over forest, (3) not connected to stone fields and <20 % cut-over forest, and (4) not connected to stone fields and >20 % cut-over forest. The sample sizes in the four settings gradually changed over the course of cycles (I-XI) due to the ongoing conversion of the landscape by forestry. The use of the threshold value of 20 % cut-over forest in the surrounding landscape was based on results from the grey-sided vole presence/absence analysis (see Fig. 4a in Paper IV).

3.3 Analytical approaches

Several analytical approaches were used in this thesis. The dependent variable was often presence/absence of voles and for such analyses logistic regression models with a binomial distribution were commonly applied (Papers II-IV). The aim was to use simple, hypothesis-driven approaches with a small number of predictor variables. However, this was not possible in all tests. For example, in the analyses of microhabitat characteristics of importance for the grey-sided vole in Paper II, many predictor variables were used and a model selection approach in the MultiModel Inference Package (MuMIn; Bartoń, 2009) in R (R

Development Core Team, 2008) was appropriate. Additionally, in a special case in Paper II when evaluating the relative importance of several variables for predicting occurrence of grey-sided vole, a Quadratic Discriminant Analysis was used (Mc Lachlan, 1992). In Paper I, several landscape metric variables such as patch size, fragmentation and core area were analysed simultaneously. Landscape metrics are often difficult to interpret since they can reveal similar landscape patterns (Cushman *et al.*, 2008) and are often inter-correlated. As such, Principal Component Analysis (PCA; Abdi *et al.*, 2010) was used to investigate which of several inter-correlated landscape variables were associated with the inland (J in Fig. 3) and coastal region (K in Fig. 3) respectively. In Paper III, there were many zero observations of voles on several sampling plots, so a multiple regression model with adjustment for zero inflation in the glmmADMB package in R was used (Fournier *et al.*, 2012). For comparisons between groups (e.g. different habitat categories), a Mann-Whitney U-test was often appropriate (Papers I-IV).

4 Results

4.1 Spatiotemporal changes in the landscape structure of forests in northern Sweden (Paper I)

Substantial changes in mean patch size of old forest were discovered. In the inland region in 1954 (J in Fig. 3), the mean patch size was approx. 90 ha in 1954 and declined gradually to 10 ha in 2005 (Fig. 5a). In the coastal region (K in Fig. 3), the mean patch size of old forest in 1954 was 30 ha and declined to approx. 5 ha in 2005 (Fig. 5b). The four investigated coniferous forest vegetation types (lichen, mesic, moist and wet forests) showed a similar trend. For example, mean patch size of old lichen type forests declined from >30 ha to <5 ha in the inland region 1954-2005. In the gap-analysis, a deficit of protected land in both the inland and coastal regions in order to fulfil the Nagoya agreement protection goal of protecting 17 % of terrestrial land was found. However, in 2005, there was enough old forest left in the landscape, but not yet formally protected, that could be incorporated into future reserve networks. The sizes of the forest patches was, however, rather small. For example, in the coastal area in 2005, more than a single >20 ha old mesic forest patch only existed in three out of eight 5×5 km sub-areas. The grey-sided vole (*Myodes rufocanus*) declined severely in the 1970-1980s and the decline coincided with a decline in mean focal patch size of old forest.

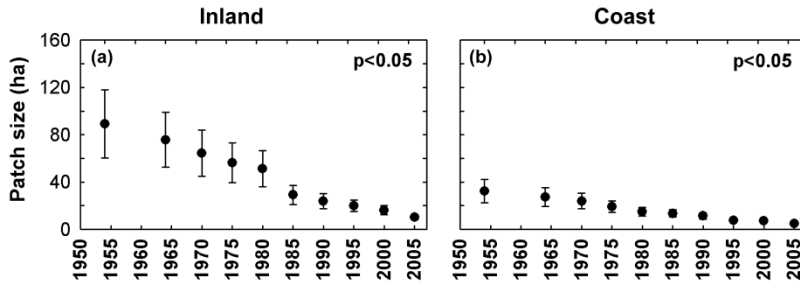


Figure 5. Temporal changes in 1954-2005 of mean patch size of old forest (mean \pm SE) in 5x5 km areas in (a) the inland (J in Fig. 3; $n = 8$) and (b) coastal (K in Fig. 3; $n = 8$) region of the study area in Västerbotten county, Sweden.

4.2 Predicting grey-sided vole occurrence in northern Sweden at multiple spatial scales (Paper II)

The results were based on grey-sided voles trapped in study area I, since no voles were trapped in study area II. The significantly shorter average distance ($p < 0.01$) from sampling plots to nearest stone fields in study area I ($1122\text{m} \pm 448$; mean \pm SE) compared with study area II ($3649\text{m} \pm 846$; mean \pm SE) may explain why no grey-sided voles were caught on sampling plots in study area II. At the habitat scale, number of large stone holes ($\phi > 5$ cm) and proportion of pine trees were the two best predictors of grey-sided vole occurrence. There was also a near linear relationship ($r = 0.74$, $p < 0.001$) between mean number of large stone holes on the sampling plots and density of grey-sided voles (Fig. 6). At the local scale, patch size of old forest was found to be linked to grey-sided vole occurrence with a substantially larger sample size than in previous studies. Connectivity of old forest was a good predictor of grey-sided vole occurrence at the landscape scale, and the predictive value increased with longer simulated grey-sided vole dispersal distances. In addition, proximity to stone fields was of high importance. When trying to estimate the relative importance of patch size of old forest, connectivity and distance from stone fields, a combination of all three variables was found to best predict *both* presence and absence of grey-sided voles. In conclusion, all three variables are needed for a good prediction of grey-sided vole occurrence in lowland boreal forests.

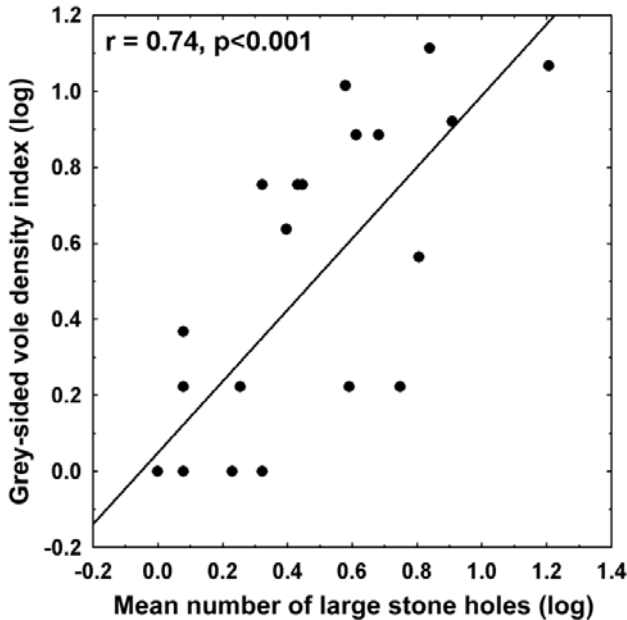


Figure 6. Grey-sided vole density index (no. of voles / 100 trap nights) against mean number of large stone holes ($\phi > 5$ cm) per sampling plot ($n = 23$) in study area I in Paper II (I in Fig. 4). The scatter plot is fitted with a linear function. The P -value denotes significance of the Pearson correlation coefficient, r .

4.3 Spatial and temporal variation of hantavirus infection in managed forest landscapes (Paper III)

At the habitat scale, PUUV infected voles usually survived low density periods of the vole cycles in old forest habitats (as in fall 1979, 1982, 1985 and spring 1983 in Fig. 7). Mires were found to be low quality habitats for both infected and non-infected voles. Infected voles never occurred on mires in spring (Fig. 7) and non-infected voles only occasionally. The density of PUUV infected bank voles (also termed infection load, IL) was significantly higher in old forests compared with cut-over forest during spring ($p < 0.05$) but not fall when considering all years. At the landscape scale, a high proportion of cut-over forest (%) in the surrounding landscape was negatively related to PUUV infected voles in spring when controlling for local habitat type and non-infected voles. In addition, a temporal difference between the two analysed vole cycles was found regarding IL. In cycle I, IL was approximately twice as high as in cycle II. To conclude, habitat and landscape properties were related to survival of PUUV and IL can change drastically for currently unknown reasons between vole cycles in any type of habitat and landscape.

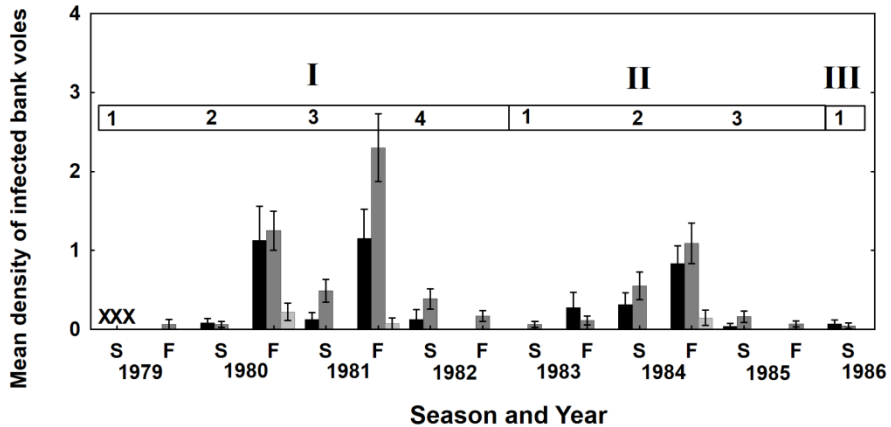


Figure 7. Mean density of PUUV infected bank voles, indexed as number of trapped individuals per 100 trap-nights (mean \pm SE) in 1979-1986, representing different phases/years (1-4) of three successive vole cycles (I-III). Three habitat categories were used, cut-over forest (black bars), old forest (dark grey bars) and mires (light grey bars). F = Fall, S = Spring. 'X' denotes that hantavirus antibodies were not analysed in spring 1979. Note that four plots with old forest were clear-cut during the study period.

4.4 Evidence for different drivers behind dampening of vole cycles across Europe (Paper IV)

At the habitat scale, grey-sided voles survived in local plots with old forests during the low density periods of the vole cycles. At the landscape scale, the decline in grey-sided vole (Fig. 8) and field vole distribution (proportion of occupied sampling plots (%)) coincided with an increase in proportion of cut-over forest (%) in the surrounding landscape. A relationship between grey-sided vole local extinction and increased proportion of cut-over forests in the surrounding landscape over time was found. In contrast, for the field vole, no such relationship was found, suggesting action of another strong driver besides forestry. In proximity to the sampling plots in the western part of the NEMP, grey-sided voles were found significantly more often in stone fields, indicating that such areas are refuge habitats for the vole. In the final analyses, information on grey-sided vole landscape requirements was used to define four different landscape settings (see section 3.2.4). In the landscape setting with <20 % cut-over forest in the surrounding landscape with maintained connectivity to forested stone fields, grey-sided voles never went extinct during the whole study period, and even showed temporary recoveries in density. In the other three landscape settings, grey-sided voles went locally extinct.

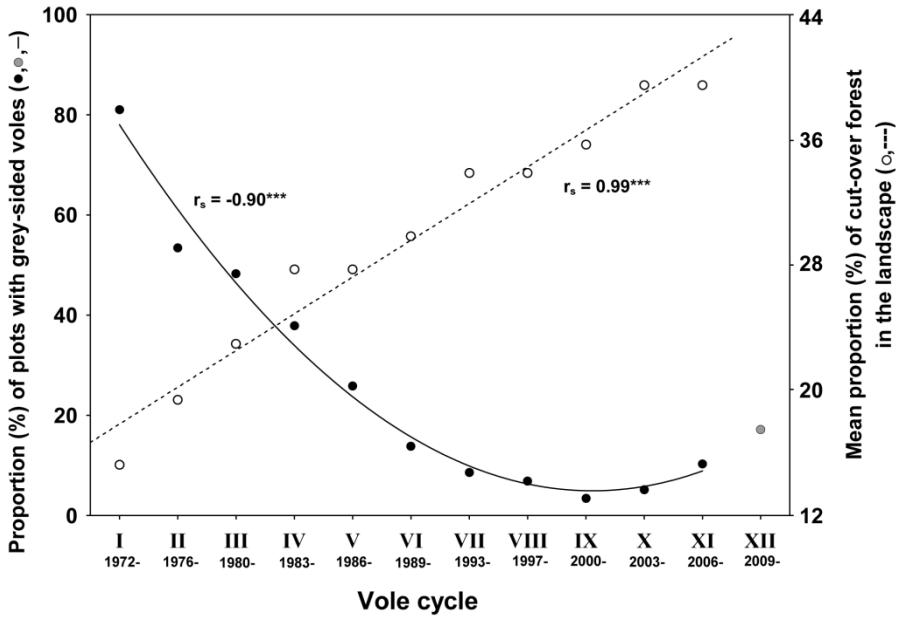


Figure 8. Proportion of sampling plots (%; $n = 58$; left axis) with grey-sided voles in cycle I-XII, 1972-2013 and mean proportional area of cut-over forest (%; $n = 58$; right axis) in the landscape surrounding each sampling plot (start year of each cycle noted in the figure). r_s = Spearman correlation coefficient in cycle I-XI (cycle XII lacks landscape data and was not included in the correlation test); *** = $p < 0.001$.

5 Discussion

The main message from this thesis is that intensive clear-cutting of old forest is linked to the decline of the grey-sided vole in northern Sweden and to spatiotemporal dynamics of PUUV. However, for the grey-sided vole, it is not only old forest that is required for its long-term survival. The species is also dependent on abiotic features such as stone fields. Using a combination of forest vegetation and geological maps with stone fields, landscape characteristics that were most strongly related to occurrence and abundance of the grey-sided vole were pinpointed. Combining geological and environmental landscape data to predict species occurrences is an approach seldom used in terrestrial landscape ecology (but see e.g. Yaacobi *et al.*, 2007). Optimal habitats for grey-sided voles are large patches of old pine forests, well connected to other patches of old forest and within close proximity of stone fields (Papers II & IV, Fig. 9).

Both old forests and especially stone fields provide small mammals with shelter. In old forests, shelter can take the form of, for example, dead wood, a scarce resource in managed forests of all age classes (Stenbacka *et al.*, 2010). As such, the measure used in Papers I, III and IV, proportion of cut-over forest in the surrounding landscape, was proven to be a powerful predictor variable and negative for occurrence of both grey-sided voles and PUUV infected bank voles.



Figure 9. Old pine forest with stone fields is an optimal habitat for the grey-sided vole in lowland boreal forests. This sampling plot yielded the highest densities of grey-sided voles in Paper II (photo: Magnus Magnusson).

The function of shelter is probably linked to a decreased predation risk from avian predators. It has been shown that Tengmalm's owl (*Aegolius funereus*) preys on grey-sided voles less than expected from their relative abundance (Hörnfeldt *et al.*, 1990). This may be an effect linked to the findings in this thesis, that grey-sided voles prefer sheltered habitats, such as stone fields, that are difficult to access for avian predators. In contrast, other specialist vole predators, such as the small weasel (*Mustela nivalis*) and stoat (*M. erminea*), regularly use stone fields and have dens in such areas (Oksanen *et al.*, 1992). However, the low nutrient status in grey-sided vole habitats may exclude both extensive mustelid predation and competition from the dominant field vole. Field voles have low abundances in stone fields (Hansson, 1978) and on nutrient poor sites in general (Viitala, 1977). Also, breeding small weasel females avoid nutrient poor sites since they are dependent on high threshold densities of field voles (Henttonen, 1987).

Grey-sided voles' main winter food plant is the dwarf shrub bilberry (*Vaccinium myrtillus*; Hambäck *et al.*, 1998). Surprisingly, the cover of bilberry had no effect on presence of grey-sided voles while stone holes providing shelter was found to be of high importance (Fig. 6). This result

indicates that grey-sided voles may select habitats based on shelter rather than amount of food. However, an alternative explanation would be that high densities of grey-sided voles reduce the biomass and quality of bilberry dwarf shrubs since the voles graze more intensively (see e.g. Dahlgren *et al.*, 2007). More studies of the relative importance of food and shelter for grey-sided vole survival in forest landscapes with different habitat composition are needed to confirm this.

Recent studies have proposed that climatic variables such as warmer winters caused the long-term dampening and decline of vole populations across Europe during the late 1980s and 1990s (Hörnfeldt, 2004; Hörnfeldt *et al.*, 2005; Ims *et al.*, 2008; Cornulier *et al.*, 2013). In Sweden there have been warmer than average winters during most of the years from 1989 until 2009 (Alexandersson, 2002). The trend was broken in 2010-11, when two cold winters (Fig. 10; Swedish Meteorological and Hydrological Institute 2014a) with a thick snow cover (Swedish Meteorological and Hydrological Institute, 2014b) coincided with high overall vole numbers (Hörnfeldt, 2014). During that time, the field vole doubled its distribution in the NEMP area and occupied >70 % of the sampling plots, a similar distribution as in the 1970s before the field vole population decline. However, the grey-sided vole distribution increased only slightly from the low levels in 1990-2000s and was still restricted to <20 % of the sampling plots, which can be compared with a distribution of >80 % in the beginning of the 1970s (Fig. 8). Field voles, in contrast to grey-sided voles that depend on suitable habitat and landscape structure, may be able to reproduce and spread quickly throughout the landscape when favorable winter conditions prevail. This conclusion is further supported by the fact that in Ammarnäs, located west of the current study area, and at a higher altitude in the Swedish mountains, where there is no large-scale forestry practices, grey-sided voles, after having very low numbers in the late 1990s, recovered strongly in the early 2000s and to much higher numbers than in the NEMP area in the 1970s before the long-term decline (Ecke *et al.*, 2010; Hörnfeldt, 2014).

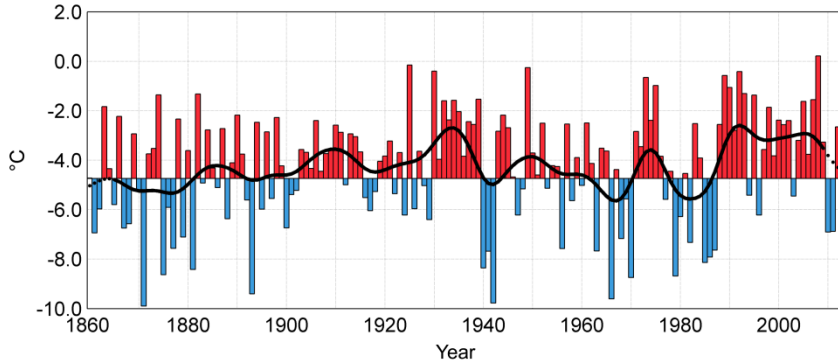


Figure 10. Winter mean temperature (December-February) 1860-2013 at 35 Swedish weather stations. Red bars shows higher and blue bars lower temperatures than the mean value for the period 1961-1990. The black curve shows a harmonized mean value (Swedish Meteorological and Hydrological Institute, 2014a).

It is probable that large scale climate changes would occur with similar timing across the 58 different sampling plots in the NEMP area. However, there are large temporal differences in the decline of the grey-sided vole population on different sampling plots belonging to different landscape settings (for definition see section 3.2.4). Grey-sided voles persist with high densities in landscapes with a low proportion of cut-over forest and maintained connectivity to stone fields (Paper IV), indicating that habitat fragmentation is the strongest driver of the decline. In addition, the prolonged period with warm winters in Sweden in 1989-2009 (Fig. 10) happened after the population decline of the grey-sided vole (Figs. 2 & 8). During the population decline there was no consistent trend, winters were both warmer than the mean in the beginning of 1970s and colder than the mean during the late 1970s and most of the 1980s (Fig. 10). However, warmer winters could have contributed to prolonging the period with constant low density and distribution of grey-sided voles in 1989-2009. In future studies, the relative importance of climate changes, in particular warmer winters, and habitat loss on the density and distribution of the grey-sided vole should be evaluated. Warmer winters may affect small mammals differently depending on the specific characteristics of the snow (i.e. snow depth, hardness and presence/absence of ice close to the ground) (Ylönen & Viitala, 1985; Kausrud *et al.*, 2008). Snow characteristics vary temporally within winters and between different years, but also spatially depending on forest structure (Horstkotte & Roturier, 2013).

Warmer winters and especially number of days with rain in winter increases NE risk for humans (Khalil *et al.*, 2014). During the warm winter 2006-2007 a

large number of rainy days in December-March coincided with a major outbreak of NE in northern Sweden with approximately 1000 human cases. One suggested hypothesis is that bank voles tend to enter buildings when ice rather than snow forms close to the ground, increasing the human risk for NE infection (Khalil *et al.*, 2014; see also Olsson *et al.*, 2009). NE is a serious health problem for humans in Sweden, especially in the north, where approximately 90 % of all diagnosed cases occur (Olsson *et al.*, 2003). Epidemiology of NE is closely linked to the temporal and spatial dynamics of the bank vole (Niklasson *et al.*, 1995; Voutilainen *et al.*, 2012), and the findings in Paper III are important for improving future human risk assessments by linking large scale forest management practices to PUUV infected bank voles.

In most of the managed landscapes within the NEMP area, large patches of old forest are rare today with a steady decrease in size since the 1950s (Paper I). Intensive clear-cutting of old forest in the surrounding landscape contributes to local extinction of PUUV in spring in some areas (Paper III). However, to prevent PUUV, clear-cutting old forest may not be appropriate. The epidemiology of PUUV is complex. By clear-cutting old forest, the sympatric and dominant grey-sided vole has disappeared almost completely from the study region (Paper IV). Consequently, PUUV prevalence in the bank vole population may gradually have increased since the 1970s due to a relaxed dilution effect (Keesing *et al.*, 2006; Paper III) from the sympatric grey-sided vole and also from the field vole that had low numbers from the late 1980s until 2010-11. Indeed, Voutilainen *et al.* (2012) found evidence for a dilution effect on PUUV prevalence in bank voles from the presence of sympatric voles and shrews. In addition, there has probably been a relaxed predation pressure on bank voles lately due to the long-term decline of a vole specialist predator, Tengmalm's owl (Hörnfeldt *et al.*, 1990; Hipkiss *et al.*, 2013; Paper III). Ostfeld & Holt (2004) suggested that predators are 'good for human health' since they may reduce the densities of zoonotic disease reservoir species in the environment.

To conclude, there may be long-term negative effects from intensive clear-cutting of old forests on PUUV persistence (Paper III) and possible positive effects on PUUV prevalence from relaxed competition by the declining, sympatric grey-sided vole (Fig. 2 and Fig. 8; Papers I, II & IV) and the field vole (Paper IV) and relaxed predation pressure from Tengmalm's owl (Paper III).

6 Future perspectives

This thesis has provided new insights on how boreal forest landscape changes have affected the grey-sided vole decline and local extinction. It has also gained knowledge on the relationship between forestry and PUUV dynamics in a bank vole population. Several new issues that will form the basis for future research objectives have emerged during my work. I present some of them below.

- Estimate the relative importance of land-use changes and climate changes on the dampening of vole cycles.
- Study dynamics of PUUV prevalence in bank vole populations in a climate gradient from the coast to the mountains in northern Sweden.
- Investigate whether the grey-sided vole decline and local extinction since the 1970s have led to a relaxed dilution effect and long-term increase of PUUV prevalence in the bank vole population.
- Estimate the relative importance of food quality and shelter on winter survival of especially the grey-sided vole but also the field vole and bank vole.
- Compare PUUV prevalence in the bank vole population and spatial distribution of PUUV during the large NE outbreak in 2006-2007 with the situation in 1979-86 (i.e. the study period in Paper III).
- If possible, investigate how Europe-wide dampening of vole cycles have affected PUUV prevalence in different bank vole populations across Europe.
- Investigate whether PUUV can affect winter survival of other species than the bank vole, in particular the grey-sided vole.

7 Sammanfattning på svenska¹

7.1 Dynamik av sorkar och Puumala hantavirus i förhållande till intensivt skogsbruk

Intensivt skogsbruk har påverkat de flesta av världens skogsekosystem och lett till biotopförluster för många specialiserade arter. I norra Sverige har kalhyggesbruket varit den dominerade skogsbruksmetoden sedan 1950-talet. Gamla, flerskiktade skogar har ersatts av unga, enkelskiktade monokulturer. I den här avhandlingen har tre cykliska sorkarter studerats i relation till kalhyggesbruket. Fokus ligger på gråsidning (*Myodes rufocanus*), men även åkersork (*Microtus agrestis*) och skogssork (*Myodes glareolus*) har studerats. Gråsidning minskade markant i täthet och utbredning under 1970- och 1980-talen. Åkersork minskade också medan skogssork, värdjur för Puumala hantavirus (PUUV) som orsakar sorkfeber (nephropathia epidemica) hos människan, inte hade en lika markant nergång som gråsidning och åkersork.

Gråsidning föredrog lokalt gamla tallskogar och blockfält. På landskapsnivå var konnektivitet av gammal skog, storlek på fläckar av gammal skog och närhet till blockfält viktigt. Den sammanlagda mängden kalhyggen sedan 1970-talet i olika landskap hade en direkt koppling till gråsidningens minskning. Åkersorkens nergång kunde inte förklaras av kalhyggesbruket men istället verkar vinterförhållanden vara viktiga. Åkersorken återkoloniserade stora delar av undersökningsområdet under 2010-2011, två år som karakteriserades av snörika och kalla vintrar.

Den sammanlagda mängden kalhyggen i det omgivande landskapet var också negativt kopplad till förekomst av PUUV-infekterade skogssorkar på våren. Infekterade sorkar överlevde bottenfaser mellan cykler i gamla skogar medan myrar visade sig vara dåliga biotoper för både infekterade och icke infekterade skogssorkar.

1. Summary in Swedish

Sammanfattningsvis konstateras att både den rumsliga och tidsmässiga variationen i täthet och utbredning av gråsiding och PUUV-infekterade skogssorkar påverkas av det intensiva kalhyggesbruket. Landskapsförändringarna orsakade av intensivt kalhyggesbruk har i den boreala skogsregionen skett parallellt med en period av varmare vintrar. Jag föreslår att framtida studier bör fokusera på att undersöka dessa två faktors relativa påverkan på populationsdynamiken hos PUUV-infekterade skogssorkar, gråsiding och åkersork.

Acknowledgments

First of all I like to thank my principal supervisor Birger Hörnfeldt for research ideas, inspiring work, fruitful discussion and several nice excursions and conferences during these last five years. I will especially remember the day in fall 2010 when we were leaving Stora Sjöfallet National Park and spotted grey-sided voles running in and out of stone holes 10 m away in the middle of the day! Another highlight was our visit to Pallasjärvi with Heikki Henttonen in 2012. I also like to give a big thank you to my assistant supervisor Frauke Ecke, especially for her dedication and knowledge in landscape ecology but also for inspiring discussions and for attending several nice excursions and conferences.

Zoonotic disease as a research subject was introduced late in my PhD by Birger and has given me valuable inspiration. I believe it is an important research topic for ecologists to work with in order to help prevent and gain deeper knowledge of human disease outbreaks. I am part of a zoonosis-group now together with Birger, Frauke, Hussein Khalil, Gert Olsson and Magnus Evander that socially and scientifically works well and is fun to work within. The nice conference in Portugal this last summer with several oral presentations from the group was a confirmation of the mutual good work we together accomplished during the last ca 1.5 years.

In the field work I have had help from several people. I especially thank Fredrik Lindgren for help with vole-trapping and the stone field inventory. I appreciate that the stone field inventory was done in such a detailed manner! I also like to thank Katie Andrle, Rory Hägglund, Arvid Bergsten, Niklas Paulsson and the regular field staff in the NEMP led by Ulf Eklund and Åke Nordström for help with trapping voles. Arvid was also an important collaborator for Paper II along with my second assistant supervisor, Örjan Bodin. That study took a long time and hard effort to finish but gave us a lot of new, important knowledge about the ecology of the grey-sided vole. Thanks

Edward Moss for being a nice room-mate and for participating on excursions looking at eagles, eagle nests and lichens. I also like to thank Hussein for interesting discussions and collaboration on several studies. Our co-operation will hopefully continue in the future! Thanks to Pernilla Christensen for sharing knowledge and literature about the grey-sided vole. Thanks also to Jean-Michel Roberge for being a good friend and I will always remember the nice conservation conference we both attended in New Zealand in 2011!

At the institution I thank all PhDs, field staff, the administration and senior scientists for various forms of input and meetings on seminars, excursions, in the fika room and during social activities. Roger Pettersson and Jean-Michel have given me the valuable opportunity to teach on both basic and advanced level courses in forest faunistics and conservation ecology. Many thanks for that! I hope to be able to continue teaching in those subjects at VFM. Jon Andersson has been a good teaching colleague and friend. I appreciate that VFM and the prefect Hans Lundqvist have been supportive in giving valuable advice for future post-doc plans and for financing some of the time during the last year needed for me to finish this thesis. Thanks to Navinder Singh and Joris Cromsigt for the good work they do as PhD-coordinators. Thanks also to Per Ljung, Kjell Danell, Heidi Hauffe, Navinder, Birger, Frauke and Karin for reading and commenting on this thesis and to Tim Hipkiss for kindly improving the English.

Lastly I thank my family. I always have your support and understanding Karin and that is extremely valuable. When our daughter Ingrid was about six months old, I very much appreciated that you could follow me out on field work and stay in small villages with Ingrid while I was out in the forest counting different sized holes in the ground day in and day out!

References

- Aars, J., Lambin, X., Denny, R. & Griffin, A.C. (2001). Water vole in the Scottish uplands: distribution patterns of disturbed and pristine populations ahead and behind the American mink invasion front. *Animal Conservation* 4, 187-194.
- Abdi, H. & Williams, L.J. (2010). Principal component analysis. *Wiley Interdisciplinary Reviews: Computational Statistics* 2(4), 433-459.
- Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5, 169-211.
- Alexandersson, H. (2002). Temperatur och nederbörd i Sverige 1860-2001 (Temperature and precipitation in Sweden 1860-2001). Meteorologi rapport 104. (In Swedish with English abstract).
- Andersson, L. (2009). Geographical vegetation data of Lantmäteriet in Sweden. In: Bryn, A., Dramstad, W., Fjellstad, W. (eds.). Viten fra Skog og landskap. Mapping and monitoring of nordic vegetation and landscapes. Ås, Norway: Norsk institutt for skog og landskap; pp. 9-12
- Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355-366.
- Angelstam, P., Roberge, J-M., Löhmus, A., Bergmanis, M., Brazaitis, G., Dönn-Breuss, M., Edenius, L., Kosinski, Z., Kurlavicius, P., Lärmanis, V. Lūkins, M., Mikusiński, G., Račinskis, E., Strazds, M. & Tryjanowski. (2004). Habitat modelling as a tool for landscape-scale conservation – a review of parameters for focal forest birds. *Ecological Bulletins* 51, 427-453.
- Angelstam, P., Jonsson, B-G., Törnblom, J., Andersson, K., Axelsson, R. & Roberge, J-M. (2010). Landskapsansats för bevarande av skoglig biologisk mångfald – en uppföljning av 1997 års regionala bristanalys, och om behovet av samverkan mellan aktörer. Skogsstyrelsen, Rapport 4/2010. Swedish Forest Agency, Jönköping, Sweden.
- Arnborg, T. (1990). Forest types of northern Sweden. Introduction to and translation of "Det nordsvenska skogstypsschemat". *Vegetatio* 90, 1-13.
- Bartoń, K. (2009) *MuMIn: multi-model inference*. R package version 0.12.2/r18. Available at: <http://R-Forge.R-project.org/projects/mumin/>.
- Brommer, J. E., Pietäinen, H., Ahola, K., Karell, P., Karstinen, T. & Kolunen, H. (2010). The return of vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. *Global Change Biology* 16, 577-586.

- Brunner-Korvenkontio, M., Vaheri, A., Hovi, T., von Bonsdorff, C.-H., Vuorimies, J., Manni, T., Penttinen, K., Oker-Blom, N. & Lähdevirta, J. (1980). Nephropathia Epidemica: Detection of Antigen in Bank Voles and Serologic Diagnosis of Human Infection. *The Journal of Infectious Diseases* 141(2), 131-134.
- Burthe, S., Telfer, S., Begon, M., Bennet, M., Smith, A. & Lambin, X. (2008). Cowpox virus infection in natural field vole *Microtus agrestis* populations: significant negative impacts on survival. *Journal of Animal Ecology* 77, 110-119.
- Carver, S., Kilpatrick, A.M., Kuenzi, A., Douglass, R., Ostfeld, R.S. & Weinstein, P. (2010). Environmental monitoring to enhance comprehension and control of infectious diseases. *Journal of Environmental Monitoring* 12(11), 2048-2055.
- Carver, S., Kuenzi, A., Bagamian, K.H., Mills, J.N., Rollin, P.E., Zanto, S.N. & Douglass, R. (2011). A temporal dilution effect: hantavirus infection in deer mice and the intermittent presence of voles in Montana. *Oecologia* 166(3), 713-721.
- Childs, J.E., Ksiazek, T.G., Spiropoulou, F.C., Krebs, J.W., Morzunov, S., Maupin, G.O., Gage, K.L., Rollin, P.E., Sarisky, J., Ensore, R.E., Frey, J.K., Peters, C.J. & Nichol, S.T. (1994). Serologic and Genetic Identification of *Peromyscus maniculatus* as the Primary Rodent Reservoir for a New Hantavirus in the Southwestern United States. *The Journal of Infectious Diseases* 169, 1271-1280.
- Christensen, P. & Hörnfeldt, B. (2006). Habitat preferences of *Clethrionomys rufocanus* in boreal Sweden. *Landscape Ecology* 21, 185-194.
- Christensen, P., Ecke, F., Sandström, P., Nilsson, M., Hörnfeldt, B. (2008). Can landscape properties predict occurrence of grey-sided voles? *Population Ecology* 50, 169-179.
- Convention on Biological Diversity. (2010). X/2 Strategic Plan for Biodiversity 2011-2020: IV Strategic goals and the Aichi biodiversity target, Target 11.
- Cornulier, T., Yoccoz, N.G., Bretagnolle, V., Brommer, J.E., Butet, A., Ecke, F., Elston, D.A., Framstad, E., Henttonen, H., Hörnfeldt, B., Huitu, O., Imholt, C., Ims, R.A., Jacob, J., Jędrzejewska, B., Millon, A., Petty, S.J., Pietiäinen, H., Tkadlec, E., Zub, K. & Lambin, X. (2013). Europe-Wide Dampening of Population Cycles in Keystone Herbivores. *Science* 340, 63-66.
- Cushman, S.A., McGarigal, K. & Neel, M.C. (2008). Parsimony in landscape metrics: strength, universality, and consistency. *Ecological Indicators* 8, 691-703.
- Dahlgren, J., Oksanen, L., Sjödin, M. & Olofsson, J. (2007). Interactions between gray-sided voles (*Clethrionomys rufocanus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. *Oecologia* 152, 525-532.
- Davis, S., Calvet, E. & Leirs, H. (2005). Fluctuating Rodent Populations and Risk to Humans from Rodent-Borne Zoonoses. *Vector-Borne and Zoonotic Diseases* 5, 305-314.
- Dearing, M.D. & Dizney, L. (2010). Ecology of hantavirus in a changing world. *Annals of the New York Academy of Science*. 1195, 99-112.
- Despommier, D., Ellis, B.R., Wilcox, B.A. (2007). The Role of Ecotones in Emerging Infectious Diseases. *EcoHealth* 3, 281-289.
- Ebeling, F. (1959). *Skogarna och deras vård i övre Norrland från och med 1930-talet*. In: Arpi, G. (Ed.) *Sveriges skogar under 100 år*. pp: 413-443, Stockholm, kungliga domänsstyrelsen.

- Ecke, F., Löfgren, O. & Sörlin, D. (2002). Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *Journal of Applied Ecology* 39, 781-792.
- Ecke, F., Christensen, P., Sandström, P. & Hörnfeldt, B. (2006). Identification of landscape elements related to local declines of a boreal grey-sided vole population. *Landscape Ecology* 21, 485-497.
- Ecke, F., Christensen, P., Rentz, R., Nilsson, M., Sandström, P. & Hörnfeldt, B. (2010). Landscape structure and the long-term decline of cyclic grey-sided voles in Fennoscandia. *Landscape Ecology* 25, 551-560.
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. Boreal ecosystems and landscapes: structures, processes and conservation of biodiversity. *Ecological Bulletins* 46, 16-47.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics* 34, 487-515.
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianello, J., Magnusson, A., Maunder, M.N., Nielsen, A. & Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27(2), 233-249.
- Grellman, D. (2002). Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos* 98(2), 190-204.
- Gu, W., Heikkilä, R. & Hanski, I. (2002). Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. *Landscape Ecology* 17, 699-710.
- Gärdenfors, U. (Ed.) (2010). The 2010 red list of Swedish species. Artdatabanken, Uppsala.
- Hambäck, P.A., Schneider, M. & Oksanen, T. (1998). Winter herbivory by voles during a population peak: the relative importance of local factors and landscape patterns. *Journal of Animal Ecology* 67, 544-553.
- Hanski, I. & Henttonen, H. (1996). Predation on Competing Rodent Species: A Simple Explanation of Complex Patterns. *Journal of Animal Ecology* 65, 220-232.
- Hansson, L. (1977). Spatial Dynamics of Field Voles *Microtus agrestis* in Heterogeneous Landscapes. *Oikos* 29(3), 539-544.
- Hansson, L. (1978). Small mammal abundance in relation to environmental variables in three Swedish forest phases. *Studia Forestalia Suecica*. 147, 1-40.
- Helle, P. & Järvinen, O. (1986). Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* 46, 107-115.
- Henttonen, H. (1987). The impact of spacing behavior in microtine rodents on the dynamics of least weasels *Mustela nivalis* – a hypothesis. *Oikos* 50, 366-370.
- Henttonen, H. (1998). The red vole, *Clethrionomys rutilus*, as an indicator of old forest in northern Lapland, in: Gustafsson, L. et al. (Ed.) (1998). *Biodiversity in managed forests - concepts and solutions, Sweden 1997: abstracts of invited papers, voluntary papers and posters, Uppsala, Sweden, May 29-31 1997. Report*, 1: pp. 98
- Henttonen, H. (2000). Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjärvi, northern Finnish taiga. *Polish Journal of Ecology* 48, 87-96.

- Hipkiss, T., Gustafsson, J., Eklund, U., Hörnfeldt, B. (2013). Is the long-term decline of boreal owls in Sweden caused by avoidance of old boxes? *Journal of Raptor Research* 47, 15-20.
- Horstkotte, T. & Roturier, S. (2013). Does forest stand structure impact the dynamics of snow on winter grazing grounds of reindeer (*Rangifer t. tarandus*)? *Forest Ecology and Management* 291, 162-171.
- Hörnfeldt, B. (1978). Synchronous population fluctuations in voles, small game, owls and tularemia in northern Sweden. *Oecologia* 32, 141-152.
- Hörnfeldt, B., Carlsson, B-G., Löfgren, O. & Eklund, U. (1990). Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). *Canadian Journal of Zoology* 68(3), 522-530.
- Hörnfeldt, B. (1994). Delayed density dependence as a determinant of vole cycles. *Ecology* 75, 791-806.
- Hörnfeldt, B. (2004). Long-term decline in numbers of cyclic voles in boreal Sweden: analyses and presentation of hypotheses. *Oikos* 107, 376-392.
- Hörnfeldt, B., Hipkiss, T. & Eklund, U. (2005). Fading out of vole and predator cycles? *Proceedings of The Royal Society B* 272, 2045-2049.
- Hörnfeldt, B., Christensen, P., Sandström, P., Ecke, F. (2006). Long-term decline and local extinction of *Clethrionomys rufocanus* in boreal Sweden. *Landscape Ecology* 21, 1135-1150.
- Hörnfeldt, B. (2014). *Miljöövervakning av smågnagare*. Last updated 2014-04-06. Available from: <http://www.slu.se/sv/institutioner/vilt-fisk-miljo/personal/lista/birger-hornfeldt/miljoovervakning-av-smagnagare/>.
- Ims, R.A., Henden, J-A. & Killengreen. (2008). Collapsing population cycles. *TRENDS in Ecology and Evolution*. 23, 79-86.
- Jacob, J., Manson, P., Barfknecht, R. & Fredricks, T. (2013). Common vole (*Microtus arvalis*) ecology and management, implications for risk assessment of plant protection products. *Pest Management Science* 70(6), 869-878.
- Johansson, L. J., Hall, K., Prentice, H.C., Ihse, M., Reitalu, T., Sykes, M.T. & Kindström, M. (2008). Semi-natural grassland continuity, long-term land-use change and plant species richness in an agricultural landscape on Öland, Sweden. *Landscape and Urban Planning* 84, 200-211.
- Josefsson, T., Hörnberg, G. & Östlund, L. (2009). Long-term human impact and vegetation changes in a boreal forest reserve: implications for the use of protected areas as ecological references. *Ecosystems* 12(6), 1017-1036.
- Kallio, E.R., Poikonen, A., Vaheri, A., Vapalahti, O., Henttonen, H., Koskela, E. & Mappes, T. (2006). Maternal antibodies postpone hantavirus infection and enhance individual breeding success. *Proceedings of the Royal Society B* 273, 2771-2776.
- Kallio, E.R., Voutilainen, L., Vapalahti, O., Vaheri, A., Henttonen, H., Koskela, E. & Mappes, T. (2007). Endemic hantavirus infection impairs the winter survival of its rodent host. *Ecology* 88(8), 1911-1916.
- Kallio, E.R., Begon, M., Henttonen, H., Koskela, E., Mappes, T., Vaheri, A. & Vapalahti, O. (2009). Cyclic hantavirus epidemics in humans – Predicted by rodent host dynamics. *Epidemics* 1, 101-107.

- Kaneko, Y., Nakata, K., Saitoh, T., Stenseth, N.C. & Bjørnstad, O.N. (1998). The Biology of the Vole *Clethrionomys rufocanus*: a Review. *Researches on Population Ecology* 40(1), 21-37.
- Kardell, L. (2004). *Svenskarna och skogen. Del 2: Från baggböleri till naturvård*. Jönköping, Swedish Forest Agency.
- Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T. & Stenseth, N.C. (2008). Linking climate change to lemming cycles. *Nature* 456, 93-97.
- Keesing, F., Holt, R.D. & Ostfeld, R.S. (2006). Effects of species diversity on disease risk. *Ecology Letters* 9, 485-498.
- Keesing, F., Belden, L.K., Daszak, P., Dobson, A., Harvell, C.D., Holt, R.D., Hudson, P., Jolles, A., Jones, K.E., Mitchell, C.E., Myers, S.S., Bogichi, T. & Ostfeld, R.S. (2010). Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468, 647-652.
- Kerr, J. T. & Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *TRENDS in Ecology and Evolution* 18(6), 299-305.
- Khalil, H., Olsson, G., Ecke, F., Evander, M., Hjertqvist, M., Magnusson, M., Ottosson-Löfvenius, M. & Hörnfeldt, B. (2014). The importance of bank vole density and rainy winters in predicting nephropathia epidemica incidence in Northern Sweden. *PLoS ONE* 9(11), e111663.
- Korpela, K., Delgado, M., Henttonen, H., Korpmimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Yoccoz, N. & Huitu, O. (2013). Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. *Global Change Biology* 19, 697-710.
- Korpmimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002). Dynamic effects of predators on cyclic voles, field experimentation and model extrapolation. *Proceedings of the Royal Society B*. 269, 991-997.
- Krebs, C.J. & Myers, J.H. (1974). Population cycles in small mammals. *Advances in Ecological Research* 8, 268-400.
- Kuussaari, M., Bommarco, R., Heikkinen, R. K., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2009). Extinction debt: a challenge for biodiversity conservation. *TRENDS in Ecology and Evolution* 24(10), 564-571.
- Langlois, J.P., Fahrig, L., Merriam, G. & Artsob, H. (2001). Landscape structure influences continental distribution of hantavirus in deer mice. *Landscape Ecology* 16, 255-266.
- Larsson, T.B. (1975). Damage Caused by Small Rodents in Sweden. *Ecological Bulletins* 19, 47-55.
- Linard, C., Lamarque, P., Heyman, P., Ducoffre, G., Luyasu, V., Tersago, K., Vanwambeke, S.O. & Lambin, E.F. (2007a). Determinants of the geographic distribution of Puumala virus and Lyme borreliosis infections in Belgium. *International Journal of Health Geographics* 6(15), 1-14.
- Linard, C., Tersago, K., Leirs, H. & Lambin, E.F. (2007b). Environmental conditions and Puumala virus transmission in Belgium. *International Journal of Health Geographics* 6(55), 1-11.

- Lindenmayer, D.B. & Franklin, J. (2002). *Conserving forest biodiversity*. Island press, Covelo, California.
- Linder, P. & Östlund, L. (1992). *Förändringar i norra Sveriges skogar 1870-1991*. *Svensk Botanisk Tidskrift* 86, 227-232.
- Lindborg, R. & Eriksson, O. (2004). Historical landscape connectivity affects present plant species diversity. *Ecology* 85, 1840-1845.
- Löfgren, O. (1995). Spatial organization of cyclic *Clethrionomys* females: occupancy of all available space at peak densities? *Oikos* 72, 29-35.
- Mc Garigal, K. & Marks, B.J. (1995). FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report, US Department of Agriculture, Forest Service, 351.
- Mc Lachlan, G.J. (1992). *Discriminant analysis and statistical pattern recognition*. John Wiley & Sons, New York.
- Meyer, B.J. & Schmaljohn, C.S. (2000). Persistent hantavirus infections: characteristics and mechanisms. *Trends in Microbiology* 8(2), 61-67.
- Mills, J.N., Yates, T.L., Ksiazek, T.G., Peters, C.J. & Childs, J.E. (1999). Long-Term Studies of Hantavirus Reservoir Populations in the Southwestern United States: Rationale, Potential, and Methods. *Emerging Infectious Diseases* 5(1), 95-101.
- Mills, J.N., Gage, K.L. & Khan, A.S. (2010). Potential Influence of Climate Change on Vector-Borne and Zoonotic Diseases: A Review and Proposed Research Plan. *Environmental Health Perspectives* 118(11), 1507-1514.
- Nagendra, H., Munroe, D.K., Southworth, J. (2004). From pattern to process: landscape fragmentation and the analysis of land use/land cover change. *Agriculture, Ecosystems and Environment* 101, 111-115.
- Niklasson, B., Hörnfeldt, B., Lundkvist, A., Björsten, S. & Leduc, J. (1995). Temporal dynamics of Puumala virus antibody prevalence in voles and of nephropathia epidemica incidence in humans. *American Journal of Tropical Medicine and Hygiene* 53(2), 134-140.
- Nilsson, S.G., Hedin, J. & Nicklasson, M. (2001). Biodiversity and its assessment in boreal and nemoral forests. *Scandinavian Journal of Forest Research* 16(Suppl. 3), 10-26.
- Odsjö, T., Bignert, A., Olsson, M., Asplund, L., Eriksson, U., Häggberg, L., Litzén, K., De With, C., Rappe, C. & Åslund, K. (1997). The Swedish Environmental Specimen Bank – Application in trend monitoring of mercury and some organohalogenated compounds. *Chemosphere* 34, 2059-2066.
- Oksanen, T., Oksanen, L. & Norberg, M. (1992). Habitat use of small mustelids in north Fennoscandian tundra: a test of the hypothesis of patchy exploitation ecosystems. *Ecography* 15, 237-244.
- Olsson, G.E., Dalerum, F., Hörnfeldt, B., Elgh, F., Palo, T.R., Juto, P. & Ahlm, C. (2003). Human Hantavirus Infections, Sweden. *Emerging Infectious Diseases* 9(11), 1395-1401.
- Olsson, G.E., White, N., Hjältén, J. & Ahlm, C. (2005). Habitat Factors Associated with Bank Voles (*Clethrionomys glareolus*) and concomitant Hantavirus in Northern Sweden. *Vector-Borne and Zoonotic Diseases* 5(4), 315-323.
- Olsson, G.E., Hjertqvist, M., Lundkvist, Å. & Hörnfeldt, B. (2009). Predicting High Risk for Human Hantavirus Infections, Sweden. *Emerging Infectious Diseases* 15(1), 104-106.

- Ostfeld, R.S. & Holt, D.R. (2004). Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. *Frontiers in Ecology and the Environment* 2(1), 13-20.
- Ostfeld, R.S., Glass, G.E. & Keesing, F. (2005). Spatial epidemiology: an emerging (or re-emerging) discipline. *TRENDS in Ecology and Evolution* 20(6), 328-336.
- Ostfeld, R.S. (2013). A Candide response to Panglossian accusations by Randolph and Dobson: biodiversity buffers disease. *Parasitology* 140, 1196-1198.
- Östlund, L., Zackrisson, O. & Axelsson, A-L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27, 1198-1206.
- Pascual-Hortal, L. & Saura, S. (2006). Comparison and development of new graph-based landscape connectivity indices: towards the prioritization of habitat patches and corridors for conservation. *Landscape Ecology* 21, 959-967.
- R Development Core Team. (2008). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-90051-07-0, URL <http://www.R-project.org>.
- Randolph, S.E. & Dobson, A.D.M. (2012). Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* 139, 847-863.
- Saitoh, T., Stenseth, N.C. & Bjørnstad, O.N. (1998). The Population Dynamics of the Vole *Clethrionomys rufocanus* in Hokkaido, Japan. *Researches on Population Ecology* 40(1), 61-76.
- Sheftel, B. & Henttonen, H. (2008). *Myodes rufocanus*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>. Downloaded on 12 September 2014.
- Shope, R. (1991). Global Climate Change and Infectious Diseases. *Environmental Health Perspectives* 96, 171-174.
- Siivonen, L. (1968). *NordEuropas däggdjur*. P.A. Norstedt and Söners förlag, Stockholm.
- Smith, M.J., White, A., Sheratt, J.A., Telfer, S., Begon, M. & Lambin, X. (2008). Disease effects on reproduction can cause population cycles in seasonal environments. *Journal of Animal Ecology* 77, 378-389.
- Stenbacka, F., Hjältén, J., Hilszczański, J. & Dynesius, M. (2010). Saproxyllic and non-saproxyllic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecological Applications* 20(8), 2310-2321.
- Stendahl, J., Lundin, L. & Nilsson, T. (2009). The stone and boulder content of Swedish forest soils. *Catena* 77, 285-291.
- Stenseth, N.C. (1999). Population Cycles in Voles and Lemmings, Density Dependence and Phase Dependence in a Stochastic World. *Oikos* 87(3), 427-461.
- Strann, K-B., Yoccoz, N.G. & Ims, R.A. (2002). Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. *Ecography* 25, 81-87.
- Suzán, G., Marcé, E., Giermakowski, J.T., Armién, B., Pascale, J., Mills, J., Ceballos, G., Gómez, A., Aguirre, A.A., Salazar-Bravo, J., Armién, A., Parmenter, R. & Yates, T. (2008). The Effect of Habitat Fragmentation and Species Diversity Loss on Hantavirus Prevalence in Panama. *Annals of the New York Academy of Science* 1149, 80-83.

- Suzán, G., Marcé, E., Giermakowski, J.T., Mills, J. N., Ceballos, G., Ostfeld, R.S., Armien, B., Pascale, J.M. & Yates, T.L. (2011). Experimental Evidence for Reduced Rodent Diversity Causing Increased Hantavirus Prevalence. *PLoS ONE* 4(5), e5461.
- Swedish Meteorological and Hydrological Institute. (2014a). Mean winter temperature (December-February) 1860-2013. Available at: <http://www.smhi.se/kunskapsbanken/vinter-1.1480>. Last accessed 21 November 2014.
- Swedish Meteorological and Hydrological Institute. (2014b). Swedish weather reports. Available at: <http://www.smhi.se/klimatdata/arssammanställningar/vader>. Last accessed 21 November 2014.
- Swedish National Forest Inventory. (2014). Areal productive forest land by age class. 1923-2012. Official Statistics of Sweden, SLU, Umeå, Sweden.
- Swedish Land Survey. (2003). Swedish CORINE Landcover Data Version 2.3. Nomenclature and Definitions. SCMD-0001.bilaga 1. Lantmäteriet, Gävle, Sweden.
- Tersago, K., Verhagen, R., Servais, A., Heyman, P., Ducoffre, G. & Leirs, H. (2009). Hantavirus disease (nephropathia epidemica) in Belgium: effects of tree seed production and climate. *Epidemiology and Infection* 137, 250-256.
- Tersago, K., Verhagen, R., Vapalahti, O., Heyman, P., Ducoffre, G. & Leirs, H. (2011). Hantavirus outbreak in Western Europe: reservoir host, infection dynamics related to human disease patterns. *Epidemiology and Infection* 139, 381-390.
- Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. & Steininger, M. (2003). Remote sensing for biodiversity science and conservation. *TRENDS in Ecology and Evolution* 18(6), 306-314.
- Viitala, J. (1977). Social organization in cyclic subarctic populations of the voles *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). *Annales Zoologici Fennici*. 14, 53-93.
- 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(6), e39452.
- Yaacobi, G., Ziv, Y. & Rosenzweig, M.L. (2007). Effects of interactive scale-dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. *Landscape Ecology* 22, 687-703.
- Yanagihara, R., Svedmyr, A., Amyx, H.L., Lee, P., Goldgaber, D., Gajdusek, D.C., Gibbs, C.J., Ström, K. (1984). Isolation and Propagation of Nephropathia Epidemica Virus in Bank Voles. *Scandinavian Journal of Infectious Diseases* 16(3), 225-228.
- Ylönen, H. & Viitala, J. (1985). Social organization of an enclosed winter population of the bank vole *Clethrionomys glareolus*. *Annales Zoologici Fennici* 22,353-358