Katri Korpela

Biological Interactions in the Boreal Ecosystem Under Climate Change

Are the Vole and Predator Cycles Disappearing?

JYVÄSKYLÄN YLIOPISTO

Katri Korpela

Biological Interactions in the Boreal Ecosystem Under Climate Change

Are the Vole and Predator Cycles Disappearing?

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2014

Biological Interactions in the Boreal Ecosystem Under Climate Change

Are the Vole and Predator Cycles Disappearing?

Katri Korpela

Biological Interactions in the Boreal Ecosystem Under Climate Change

Are the Vole and Predator Cycles Disappearing?

UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2014

ABSTRACT

Korpela, Katri
Biological Interactions in the Boreal Ecosystem Under Climate Change – Are the Vole and Predator Cycles Disappearing?
Jyväskylä: University of Jyväskylä, 2014, 57 p.
(Jyväskylä Studies in Biological and Environmental Science
ISSN 1456-9701; 291)
ISBN 978-951-39-5845-9 (nid.)
ISBN 978-951-39-5846-6 (PDF)
Yhteenveto: Ilmastonmuutoksen vaikutukset biologisiin vuorovaikutuksiin pohjoisen havumetsävyöhykkeen eliöyhteisöissä
Diss.

Due to climate change, the last 30 years have likely been the warmest in 1400 years. Incidentally, since the 1980s, animal population cycles have been collapsing in Europe. Previously, vole populations in northern Europe have undergone regular, high-amplitude fluctuations in density, reflected in the breeding success of many predators, in the composition of plant communities, in crop damage, and in the incidence of zoonotic diseases in the human population. Alarmingly, a pan-European dampening of rodent cycles was recently reported, and climate change is a potential contributor. However, although climate is considered an important factor shaping predator-vole interactions and thereby vole population dynamics, very little is currently known about the influence of climate on these phenomena. Using observational animal population and climate data collected throughout Finland during 1970-2011, I analysed the spatiotemporal variation in and the influence of climate on vole population dynamics and the interactions between voles and specialist, generalist, and avian predators. I built and validated a climate-based model for predator-vole interactions and used the model to predict how predator and vole population dynamics will respond to climate change. Climate had a profound and intricate influence on the interactions between predators and voles, and most importantly, could explain the observed geographical and temporal variation in predator-vole interactions, and in vole population dynamics. Most of the observed changes in vole population dynamics could be attributed to climate-dependent changes in the interactions between voles and the small mustelids: the small mustelids appeared to create delayed density dependence during winters in cold climates, and during summers in high-precipitation climates. According to the climate-based predator-vole interaction model, the highly regular and predictable vole cycle is likely to disappear, although in many regions, cyclicity is may persist and even strengthen in the near future.

Keywords: Climate change; *Martes*; *Microtus*; *Mustela*; *Myodes*; Population dynamics; *Vulpes.*

Katri Korpela, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address   Katri Korpela
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
katri.e.korpela@jyu.fi

Supervisors   Dr. Otso Huitu
Metla Suonenjoki
Juntintie 154
FI-77600 Suonenjoki
Finland

Dr. Esa Koskela
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Dr. Janne Sundell
Lammi Biological Station
Pääjärventie 320
FI-16900 Lammi
Finland

Reviewers   Prof. Nils Chr. Stenseth
P.O. Box 1066
Blindern 0316 Oslo
Norway

Dr. Bodil Elmhagen
Department of Zoology
SE-10691 Stockholm University
Sweden

Opponent   Prof. Herwig Leirs
Department of Biology
University of Antwerp
Belgium

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV. I was responsible for the design of the studies, for the analysis of the data, and for writing the papers. The co-authors contributed data (H. Helle, H. Henttonen, O. Huitu, E. Korpimäki, H. Pietiäinen, J. Valkama), supervised the statistical analyses (O. Ovaskainen, N. Yoccoz), and participated in writing the papers.

I   Korpela K., Delgado M., Henttonen H., Korpimäki 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.

II   Korpela K., Helle P., Henttonen H., Korpimäki E., Koskela E., Ovaskainen O., Pietiäinen H., Sundell J., Valkama J. & Huitu O. 2014. Predator-vole interactions in northern Europe: the role of small mustelids revised. Manuscript.

III   Korpela K., Helle P., Henttonen H., Korpimäki E., Koskela E., Ovaskainen O., Pietiäinen H., Sundell J., Valkama J. & Huitu O. 2014. Climate as a determinant of predator-vole interactions in the boreal ecosystem. Manuscript.

IV   Korpela K., Helle P., Henttonen H., Korpimäki E., Koskela E., Ovaskainen O., Pietiäinen H., Sundell J., Valkama J. & Huitu O. 2014. Predicting the population dynamics of voles in the boreal ecosystem under climate change. Manuscript.

1   INTRODUCTION

1.1   Climate change and trophic interactions

Global temperatures have been rising throughout the 20th century, and especially rapidly since the 1970s, as a consequence of anthropogenic greenhouse gas emissions (Stocker *et al.* 2013). The increase in temperature has been especially pronounced in the northern latitudes, and during winters and springs (Serreze *et al.* 2000). Throughout the boreal and arctic regions, temperature and precipitation have increased over the last 100 years, the extent of snow cover and sea ice decreased, glaciers reduced in size, and permafrost warmed in many places (Serreze *et al.* 2000). In Finland, the average winter, spring, summer, and autumn temperatures have increased by 1.0°C, 1.6°C, 0.4°C, and 0.7°C, respectively, since the beginning of the 20th century (Tietäväinen *et al.* 2010). The different greenhouse gas emission scenarios predict a rapid increase in temperatures in Finland over the next few decades (Jylhä *et al.* 2009). The average winter temperatures are predicted to be 2.5°C higher and the average summer temperatures 1.2°C higher in 2011-2040, as compared to 1970-2000 (Jylhä *et al.* 2009). Precipitation is predicted to increase, as well, by ca. 10% in winter, and 5% in summer.

In northern Europe, spring temperatures are rising the fastest (Jylhä *et al.* 2009, Tietäväinen *et al.* 2010, Fig. 1), which will advance the onset of snowmelt (Jylhä *et al.* 2008, Kellomäki *et al.* 2010), and the initiation of the growing season (Jylhä *et al.* 2009). From an ecological perspective, this is likely to have widespread consequences, as boreal animal and plant species time their annual cycle of reproduction according to spring conditions. Globally, advancements of spring phenology (the timing of life-cycle events) have been observed in various taxa (Ahas *et al.* 2002, Walther *et al.* 2002, Parmesan and Yohe 2003, Menzel *et al.* 2006). As different species respond to different cues – e.g. temperature, snowmelt, food availability, photoperiod – trophic mismatches are beginning to develop: species on different trophic levels change their spring phenology at different paces, often causing a previously existing temporal

synchrony between reproduction and food availability to disappear (Edwards and Richardson 2004, Post and Forchhammer 2008, Both *et al.* 2010). For many species, the changes in spring climate are thus leading to a situation where the offspring are born or hatched at a time when food availability has not reached its peak, or when temperatures may still be cold, potentially leading to lower offspring survival (Both *et al.* 2006, Lehikoinen *et al.* 2009).

As spring arrives earlier and summers become warmer, growing seasons get longer and net primary productivity (NPP) is predicted to increase substantially in northern Europe (Koca *et al.* 2006). Primary productivity in the boreal zone is limited by low temperatures, short growing seasons, CO_2 and N (Kellomäki *et al.* 1997, Nemani *et al.* 2003), and increases in NPP in northern regions are already evident (Nemani *et al.* 2003, Zhao and Running 2010). Biodiversity tends to increase with productivity and temperature (Gaston 2000, Chase and Leibold 2002), and the boreal region is expected to become increasingly important for the conservation of global biodiversity (Fischlin *et al.* 2007). However, boreal forests are likely to face increasingly severe disturbances. According to the IPCC (Intergovernmental Panel for Climate Change), boreal forests are among the most vulnerable ecosystems, whose structure and functioning is threatened by climate change (Fischlin *et al.* 2007). As temperatures rise, evapotranspiration increases, but precipitation may not increase at the same pace, especially during the next few decades (Jylhä *et al.* 2009). Furthermore, the frequency of heavy rains during summer is predicted to increase, which suggests that summers may become predominantly dry, with occasional heavy rains (Jylhä *et al.* 2009). Consequently, soil moisture content is predicted to decline during summers (Kellomäki *et al.* 2010). This may to some extent curb the increase in primary productivity, especially in northeastern Europe (Höglind *et al.* 2013). Furthermore, the intensity, severity and extent of wild fires and pest and pathogen damage in boreal forests are predicted to increase, and act synergistically with drought (Ayres and Lombardero 2000, Volney and Fleming 2000, Soja *et al.* 2007).

Autumns in northern Europe are predicted to become longer, warmer, cloudier, and rainier (Jylhä *et al.* 2009). However, plant growth is limited during late autumns by the short photoperiod, which means that the increasing autumn temperatures do not affect primary productivity as much as by the increasing spring temperatures. The onset of snow cover will occur later and the period of unstable and wet weather conditions will persist longer. In the southernmost parts of Finland, the thermic winter season (average daily temperatures continuously <0°C) will eventually be completely replaced by a long autumn (Jylhä *et al.* 2009). Already during the next few decades, winters are predicted to become milder, the number of freezing-point days (days during which temperature crosses 0°C) to increase, and the duration of snow cover to decrease (Jylhä *et al.* 2008, Kellomäki *et al.* 2010). However, even though temperatures are rising, snow depth is not predicted to decline considerably until the latter part of the century, due to the increase in precipitation (Kellomäki *et al.* 2010). The quality of snow is likely to change, as there will be more rain-on-snow and thaw-freeze events (Jylhä *et al.* 2008).

Because of the changing environmental conditions, changes in the structure and functioning of the boreal ecosystem are expected, although in Finland, extensive changes in forest cover or forest type are not expected to occur over the current century (Fischlin *et al.* 2007). In response to increasing temperatures, shorter and milder winters, and increasing productivity, the ranges of many currently temperate species may extend northward (Parmesan *et al.* 1999, Walther *et al.* 2002, Parmesan and Yohe 2003). Composition of plant and animal communities is thus expected change in the boreal region (Koca *et al.* 2006, Thuiller *et al.* 2006, Thakur *et al.* 2014, Virkkala and Lehikoinen 2014). Climate-induced range shifts are likely to cause temporal and spatial mismatches between interacting species (Schweiger *et al.* 2008) and create novel interactions between previously allopatric species.

The changes in the biotic environment are likely to influence the structure and functioning of ecosystems much more than the changes in the abiotic environment alone would, as species abundances and temporal dynamics are highly sensitive to trophic interactions, competition, and mutualistic relationships (Stenseth *et al.* 2002, Ims and Fuglei 2005, Gilman *et al.* 2010, Van der Putten *et al.* 2010). Trophic interactions are a crucial driving force of population dynamics (Berryman 2002), suggesting that climate-induced alterations in trophic interactions may influence the population dynamics of the interacting species (Stenseth et al. 2002, Kausrud et al. 2008) with potentially dramatic ecosystem-level consequences . Many species in the boreal and arctic regions exhibit cyclic population dynamics, which are often dependent on climate and thought to arise from trophic interactions (Angelstam *et al.* 1985, Stenseth *et al.* 1999, Ayres and Lombardero 2000, Klemola *et al.* 2002, Ims and Fuglei 2005). Furthermore, many of the cyclically fluctuating species are agricultural and silvicultural pests (Ayres and Lombardero 2000, Huitu *et al.* 2009), or reservoirs of zoonotic diseases (Kallio *et al.* 2009, Rossow *et al.* 2014). Understanding the climate-dependence of boreal population cycles and the associated trophic interactions is an important step towards preparation and mitigation of the potentially detrimental ecological consequences of climate change.
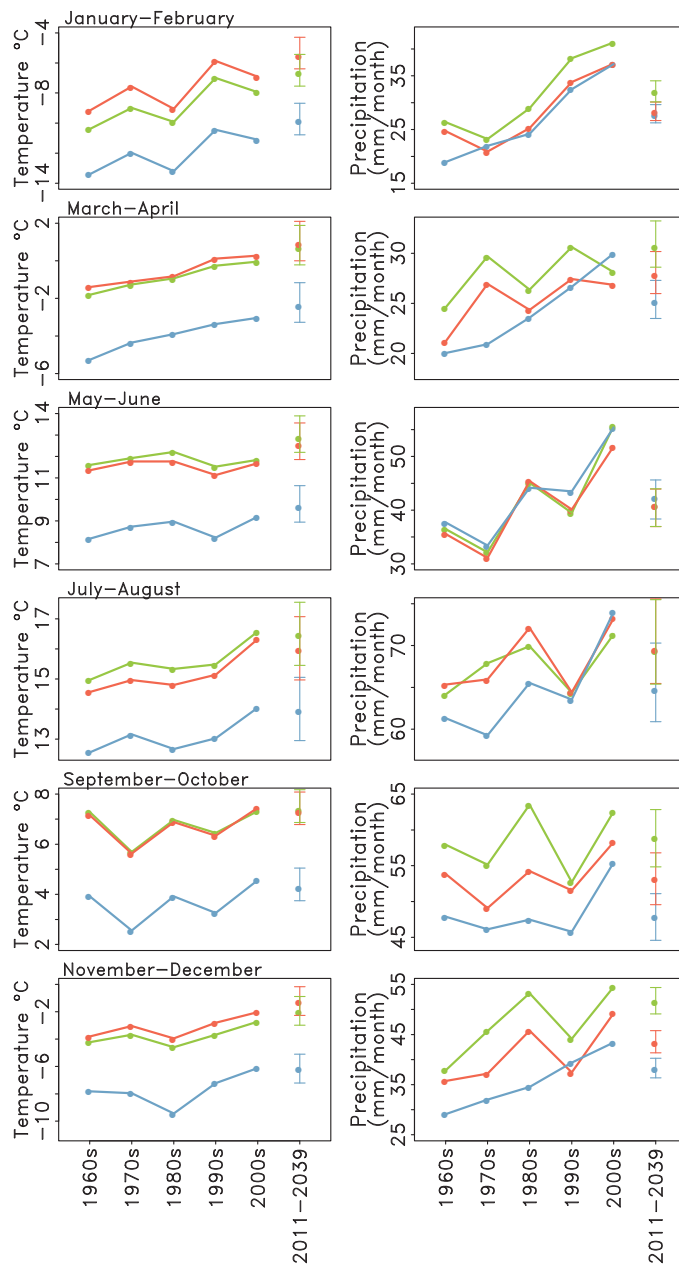
FIGURE 1   Observed and predicted average temperature and precipitation in three regions in Finland: southwest (red, 60-64°N and 20-26°E), southeast (green, 60-64°N and 26-33°E), and north (blue; 64-70°N and 20-30°E). The values are observed decadal averages (1960s-2000s) and predicted median (± predicted range) for the time period 2011-2039 (Jylhä *et al.* 2009).

1.2 Biological interactions, density dependence, and population dynamics

Population dynamics refers to the temporal pattern of population density fluctuations. Essentially, the fluctuations in population density depend on three types of factors influencing the population: random occurrences and variations in the environment, such as variations in weather; regular environmental events, such as seasonality; and biological interactions (Royama 1992, Berryman 2002). Predictable environmental variation will tend to induce predictable fluctuations in population density, in the boreal ecosystem most obviously the omnipresent pattern of summer increases and winter declines in population densities. Random environmental variation will induce irregular and unpredictable fluctuations in the absence of the other factors, but when acting in combination with predictable sources of variation or biological interactions, will increase the amplitude of the fluctuation (Royama 1992, Fig 2a).

In contrast to the impacts of the abiotic environment, the biotic environment tends to interact with the focal population in feedback loops, which may be exceedingly complex and give rise to a wide range of population fluctuations (Royama 1992, Berryman 2002). In general, a high population density will induce adverse biological interactions, such as increased competition for of food or breeding territories, increased spread of pathogens and increased abundance of predators, eventually causing a decline in population density (Tanner 1966, Brook and Bradshaw 2006). Intra- and interspecific biological interactions thus give rise to the phenomenon known as density dependence of population growth: population density influences the biotic environment, which in turn influences population growth (e.g. Hansen *et al.* 1999). The relative importance of different biotic interactions varies between populations and influences the population dynamics of the interacting species. Cyclic population dynamics, i.e. regular, predictable, multiannual fluctuations in population density, arise when the magnitude, direction (negative vs. positive), and time lag of density dependence fulfil certain requirements (Royama 1992). Multiannual cyclicity emerges when a population is influenced by negative delayed density dependence: a high population density causes a decline in population growth rate, not immediately, but after a time lag. Such time lags are inherent in many types trophic interactions (see below).

A commonly utilized way to characterize population dynamics is to estimate the direct density dependence (the influence of the current population density on the current population growth rate), and the delayed density dependence (the influence of a past density on the current population growth rate). These values can be plotted against each other to form a so-called Royama triangle (Royama 1992, Fig. 2b). All sustainable populations fall within the triangle. Under the dashed parabola, populations exhibit multiannual cyclicity. The cycle becomes longer, i.e. the time from one population peak to the next increases, as direct density dependence becomes weaker (towards the right side

12

of the triangle). The cycle becomes increasingly irregular, as delayed density dependence approaches zero. Above the parabola, on the right side of the triangle, populations are governed by irregular dynamics, and on the left, populations show a regular 2-year cycle. Temporal autocorrelations, i.e. correlations between the current population density and past population densities at different time lags, are another useful diagnostic (Fig. 3). In cyclic populations, the current population density correlates positively with the population density one cycle period ago (Fig. 3a,d). As the cycle becomes less regular, the autocorrelations weaken (Fig. 3b,d).
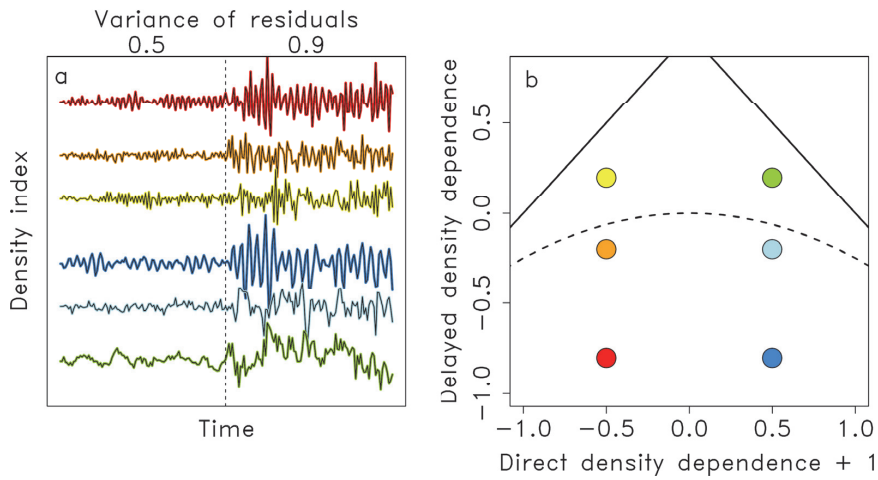
FIGURE 2   Simulated time series with different amounts of stochastic variation (a) and density dependence (b). Time series in panel a correspond to the density dependence values of the same colour in panel b.
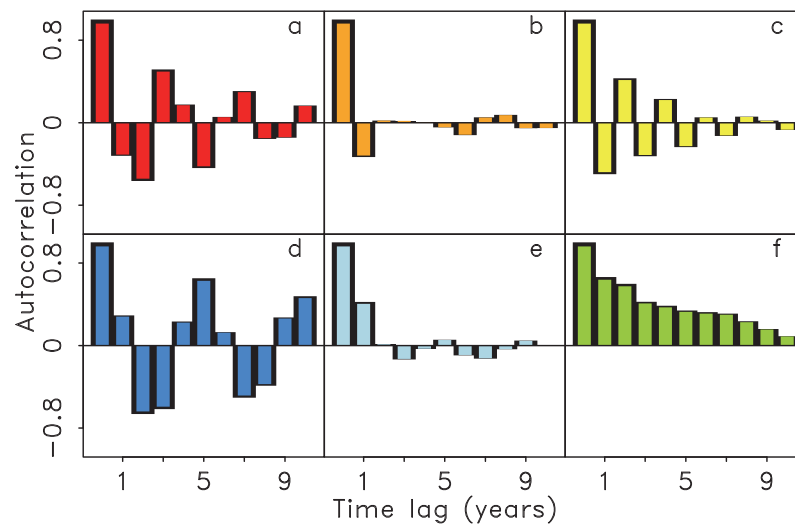
FIGURE 3   Temporal autocorrelation plots for the time series shown in Fig. 2, with corresponding colours.

1.3   The boreal vole cycle

Small rodent communities in northern Europe are subject to strong multiannual fluctuations in density (Henttonen *et al.* 1977, Hansson and Henttonen 1985, Hansson and Henttonen 1988). The boreal vole cycle is characterized by a regular sequence of the low, increase, and peak phases (Fig. 4): in the low year, vole population densities crash during winter and may continue to decline during summer and the following winter, resulting in extremely low densities. The low phase may last one or two years, after which the population densities begin to increase. The increase phase, which may again take one to two years, is followed by the peak phase, during which vole population densities are relatively high even in spring, increase through the summer, to reach very high levels in autumn. The following winter after a peak autumn again leads to the dramatic decline of population densities and to another low phase. The interval between peak densities, i.e. the cycle period, has been shown to increase with latitude, being ca. 3 years in southern Fennoscandia and 5 years in northern Finland (Hansson and Henttonen 1985).
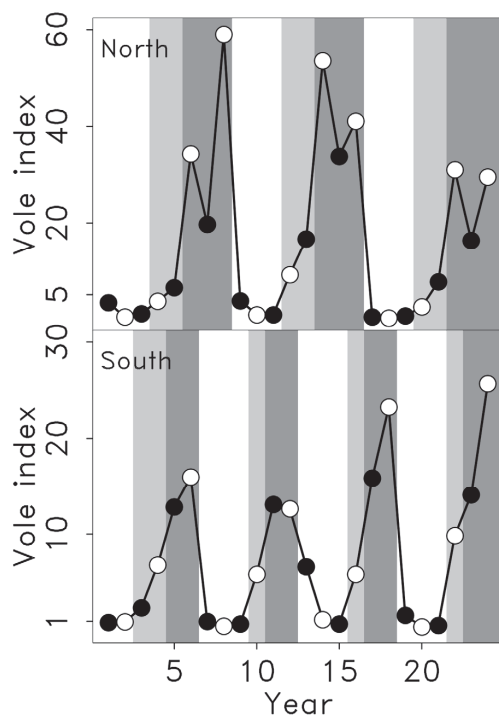
FIGURE 4   Example sections of vole population fluctuations in northern and southern Finland (I). White symbols represent autumn vole densities and black symbols spring densities. The background is coloured according to the cycle phase: white = decline/low; light grey = increase; dark grey = peak. The vole index is calculated as number of voles/100 trap nights.

Voles of the genera *Microtus* and *Myodes* form the overwhelming majority of small rodents in Finland and fluctuate in synchrony (Henttonen *et al.* 1977, Hansson and Henttonen 1988, Huitu *et al.* 2004, Korpimäki *et al.* 2005). Due to their ubiquity, abundance and regularly fluctuating densities, these two genera are the most important group of rodents, ecologically and in terms of their impact on the human society (Hörnfeldt 1978, Sundell *et al.* 2004, Huitu *et al.* 2009, Kallio *et al.* 2009). The most common mammal in Finland is the bank vole, *Myodes glareolus*, which inhabits forested habitats nearly throughout the country, being absent only in the northernmost regions where two related species, the red vole *Myodes rutilus* and the gray-sided vole *Myodes rufocanus*, replace it. The field vole, *M. agrestis*, is the most ubiquitous of the voles, inhabiting grassy fields throughout the country. In western Finland *M. agrestis* is accompanied by the sibling vole, *M. levis*, and in northern Finland by the root vole, *M. oeconomus*.

Cyclic small rodent population dynamics have been reported in the boreal zones throughout the world, as well as in temperate Europe (Saitoh *et al.* 1998, Salamolard *et al.* 2000, Tkadlec and Stenseth 2001, Cheveau *et al.* 2004, Lambin *et al.* 2006, Bobretsov 2009, Zub *et al.* 2012). Furthermore, geographic gradients in cyclicity, which appear to result from gradients in seasonality, have been described in Fennoscandia (Hansson and Henttonen 1985), central Europe (Tkadlec and Stenseth 2001), and Hokkaido, Japan (Stenseth *et al.* 1996, Stenseth *et al.* 1998). In northern Europe, the amplitude of the cycle increases towards the north, due to the extremely low vole densities during the low phase in the north (Hanski *et al.* 1994). Long winters (Hansson and Henttonen 1985, Hansson 1999), or conversely short growing seasons (Taylor *et al.* 2013), are thought to be required for cyclic vole dynamics, which indicates that the vole cycle is sensitive to climatic variations and seasonality – both of which are changing in the boreal regions due to climate change. The length of the winter season is suggested to strengthen the cyclicity by reducing the influence of the cycle-dampening generalist predators (Hansson and Henttonen 1985, Hansson 1987), increasing the time lags in the numerical responses of the predators (Norrdahl and Korpimäki 2002), or by shortening the breeding season (Taylor *et al.* 2013).

1.4 Candidate explanations for the vole cycle

To explain the vole cycle, one has to identify biological interactions, which are able to create density dependence of vole population growth. Negative direct density dependence may arise from intra-specific competition among voles for food (Huitu *et al.* 2003), and breeding territories (Bujalska 1985), antagonistic behaviour such as infanticide (Korpela *et al.* 2010), and increased prevalence of diseases (Soveri *et al.* 2000, Niklasson *et al.* 2006). However, the crucial – and more enigmatic – parameter is delayed density dependence. There has to be a feedback mechanism, which limits population growth, not immediately, but with a delay. Time lags are inherent in many interspecific interactions, but the

exact ecological mechanism causing negative delayed density dependence in vole populations is subject to a long-standing debate (reviewed in Stenseth 1999, thereafter discussed e.g. in Lambin *et al.* 2000, Hanski *et al.* 2001, Oksanen *et al.* 2001, Korpimäki *et al.* 2002, Kent *et al.* 2005, Korpimäki *et al.* 2005, Lambin *et al.* 2006, Smith *et al.* 2006, Massey *et al.* 2008, Smith *et al.* 2008, Inchausti and Ginzburg 2009, Krebs 2013).

Several hypotheses have been prosed over the decades. Currently, the following hypotheses continue to receive attention: predation by specialist predators (Hanski *et al.* 1991, Hanski and Henttonen 1996, Hanski *et al.* 2001, Korpimäki *et al.* 2002, Korpimäki *et al.* 2005), predation in combination with social factors (Andreassen *et al.* 2013), delayed effect of density on food quality (Massey *et al.* 2008, Reynolds *et al.* 2012, Selås *et al.* 2013), delayed effect of density on disease prevalence (Cavanagh *et al.* 2004, Burthe *et al.* 2006), disease-induced delay of maturation (Smith *et al.* 2008); and the delayed effect of density on life-history characteristics, mainly with respect to reproduction (Beckerman *et al.* 2002, Smith *et al.* 2006, Helle *et al.* 2012).

Shorrocks *et al.* (1998) suggested that young voles postpone the initiation of reproduction during high vole densities, leading to density-dependent age at first reproduction. Following this notion, Helle *et al.* (2012) reported that the juvenile environment influences reproduction in a density-dependent manner. However, they showed the delayed density-dependent life-history effect to be positive, i.e. to have a stabilizing effect on vole population dynamics: females born in high-density populations started breeding earlier in the following spring and produced larger litters than females born in low-density populations. Furthermore, while research in northern England has shown that the length of the breeding season does vary in response to earlier population density to the extent that could explain the multiannual vole cycle (Smith *et al.* 2006, Ergon *et al.* 2011), the cause of the delayed density dependence of breeding season length was not an intrinsic life-history characteristic but rather mediated by the environment (Ergon *et al.* 2011), i.e. a trophic interaction. To conclude, there is currently little conclusive evidence for negative intrinsic delayed density dependence in vole populations.

Studies in northern England (Massey *et al.* 2008, Reynolds *et al.* 2012) have shown that the interaction between field voles and their food plant, *Deschampsia caespitosa*, can cause negative delayed density dependence. Grazing by voles during high vole density induces the plant to accumulate silica in its tissues, which lowers its digestibility and thus has a negative effect on the herbivore population dependent on it. The silica defences remain elevated for over 6 months (Reynolds et al. 2012). Along the same lines, Selås *et al.* (2013) reported that bank vole populations in southern Norway follow blueberry reproduction with a 1-year lag, suggesting that secondary metabolites are involved. However, similar phenomena have not been observed in Finland (Laine and Henttonen 1987, Klemola *et al.* 2000). In northern Finland and Norway, the nutritional value of blueberry, an important food source for *Myodes* voles, has been shown increase, rather than to decrease, in response to *Myodes* grazing (Laine and Henttonen 1987, Dahlgren *et al.* 2007). Although some populations

of voles may be affected by food-induced negative delayed density dependence, it is questionable whether sustained anti-herbivory defences are ubiquitous enough to have a real-life effect on multispecies vole communities, feeding on various food plants, and in different habitats.

Viral diseases have been proposed as potential agents of negative delayed density dependence in vole populations, acting through sustained reduction in fecundity (Telfer *et al.* 2005, Smith *et al.* 2008) or increased mortality in the presence of other stressors (Niklasson *et al.* 2006, Kallio *et al.* 2007). Smith et al. (2008) created a host-parasite model to predict vole-cowpox dynamics, and showed that field vole population cycles in northern England, but not realistically in Fennoscandia, could be produced by the host-parasite interaction. Various pathogens are prevalent and cause mortality or reduced survival in Fennoscandian vole populations (Soveri *et al.* 2000, Niklasson *et al.* 2006, Kallio *et al.* 2007), but there are currently no data on their long-term effects on vole population dynamics.

In the boreal ecosystem, only one mechanism, predation, has gained both experimental and theoretical support, although the interpretation of and the confidence in the evidence vary between researchers (e.g. Korpimäki *et al.* 2005, Lambin *et al.* 2006, Krebs 2013). Theoretically, predators whose density increases sufficiently slowly in response to a high vole density, and that exert a strong predation pressure on voles, have the potential to create negative delayed density dependence and hence cyclic population dynamics in their prey. The small mustelids, particularly the least weasel, *Mustela nivalis*, and to an extent the stoat, *Mustela erminea,* are specialized and effective predators of small rodents (Korpimäki *et al.* 1991, Norrdahl and Korpimäki 1995). They are strongly dependent on small rodents but their reproductive rate is much slower than that of their prey, so their population densities increase in response to increasing vole densities in a delayed manner (Korpimäki *et al.* 1991, Sundell *et al.* 2013). The small mustelids are therefore considered a necessary factor for cyclic vole dynamics in Fennoscandia (Henttonen *et al.* 1987, Hanski *et al.* 2001, Korpimäki *et al.* 2005).

Generalist mammalian predators are thought to have a stabilizing influence on vole population dynamics, as they prey on voles mainly when vole densities are high, subsisting on alternative prey when voles are scarce (Andersson and Erlinge 1977, Erlinge *et al.* 1991, Hanski *et al.* 2001). Furthermore, generalist predators also prey on the small mustelids (Dell'Arte *et al.* 2007), thus potentially further weakening the specialist predator-vole interaction (Oksanen *et al.* 2001). In Finland, the red fox and the pine marten are generalist predators, which include a large share of voles in their diet (Pulliainen and Ollinmaki 1996, Dell'Arte *et al.* 2007). The generalists, whose abundance decreases northwards, are though to inhibit cycles in southern Fennoscandian vole populations, creating a latitudinal gradient of in cyclicity (Hansson and Henttonen 1985, Erlinge 1987, Klemola *et al.* 2002).

Avian predators have a strong impact on vole populations as well, but they may respond with or without a delay to vole abundance. The nomadic or migratory species (long-eared owl, short-eared owl, pygmy owl, European

kestrel, hen harrier, rough-legged buzzard, common buzzard) have the ability to track vole abundance over large areas, potentially reacting to changes in vole densities rather rapidly (Korpimäki and Norrdahl 1991a), but may also make nesting decisions based on last autumn's vole abundance (Hörnfeldt *et al.* 1990, Norrdahl and Korpimäki 2002). The reproduction, survival, or recruitment of the resident species (tawny owl, ural owl, eagle owl, Tengmal's owl) depends on autumn vole abundance (Brommer *et al.* 2002, Hakkarainen *et al.* 2002, Karell *et al.* 2009), and the population size of wintering birds follows vole abundance with a 1-year lag (Solonen 2005). Therefore, the avian predators have been suggested to contribute to the delayed density dependence in vole populations (Hörnfeldt 1994, Norrdahl and Korpimäki 2002). However, many avian predators frequently catch small mustelids (Korpimäki and Norrdahl 1989a), thus potentially weakening their interaction with the vole population and reducing cyclicity (Korpimäki and Norrdahl 1989b, Oksanen *et al.* 2001).

To conclude, vole population fluctuations are influenced by multiple inter- and intraspecific interactions. When population densities are high, intraspecific competition for food and territories, aggression, and infanticide increase (Andreassen *et al.* 2013). Predation pressure increases, as the generalist predators begin to focus on voles (Helldin 1999, Dell'Arte *et al.* 2007), and the nomadic avian predators aggregate in regions with high vole abundance (Korpimäki and Norrdahl 1991b) and limit vole population growth (Korpimäki and Norrdahl 1991a). Voles are dispersing and mobile, which increases their predation risk (Norrdahl and Korpimäki 1998). Diseases spread in high-density populations (Niklasson *et al.* 2006). Scarcity of high-quality food may limit reproduction (Forbes *et al.* 2014). Thus, mortality increases and reproduction decreases probably due to multiple synergistic causes, which together curb population growth and may initiate the decline. By the time the vole population density reaches its peak, the high abundance of voles has induced an increase in the small mustelid populations (Sundell *et al.* 2013) and promoted the reproduction of resident avian predators (Brommer *et al.* 2002, Lehikoinen *et al.* 2011). The specialist predators exert a strong predation pressure and induce the steep crash of vole population density. As the specialist predators have little alternative prey, they are forced to subsist on the declining food supply, causing increasingly intense predation pressure and reducing vole densities to an extreme low level (Korpimäki *et al.* 1991, Norrdahl and Korpimäki 1995, Klemola *et al.* 2000). Eventually the vole density is too low to sustain the predators, causing a decline in the predator densities and in predation pressure, and allowing the vole population to begin increasing again.

It is worth noting, that the lemming (Norway lemming, *Lemmus lemmus*) cycle in arctic and alpine regions of Fennoscandia is qualitatively different from the boreal vole cycle and beyond the scope of this thesis. The trophic interactions and climatic patterns associated with the lemming cycle have been extensively investigated (e.g. Oksanen and Oksanen 1992, Turchin *et al.* 2000, Kausrud *et al.* 2008, Ims *et al.* 2011). Lemming peaks are dependent on winter breeding, which occurs only during long and cold winters, when the food plants (mosses) have recovered from the previous peak (Turchin *et al.* 2000),

and the vole density is high (Ims *et al.* 2011). Hence, climate change may influence lemming populations directly (Kausrud *et al.* 2008) but also indirectly, via altered vole and predator dynamics.

1.5   Climate and the collapsing vole cycle

Recently, a European-wide dampening of population cycles has been reported, encompassing populations of *Microtus*, *Myodes,* and *Lemmus*, forest grouse, and insect herbivores (Ims *et al.* 2008, Cornulier *et al.* 2013). These large-scale alterations are expected to influence a number of predator species, many of them already facing difficulties due to climate change and habitat loss (Hörnfeldt *et al.* 2005, Millon *et al.* 2014). Considerable effects on plant communities are expected, as well, as vole grazing has a major impact on the vegetation (Rydgren *et al.* 2007, Olofsson *et al.* 2012). The cause of these changes is unknown, although many hypotheses have been presented (Hörnfeldt 2004), of which climate change has received the most support (Bierman *et al.* 2006, Ludwig *et al.* 2006, Esper *et al.* 2007, Kausrud *et al.* 2008). Because of the extent of the syndrome, encompassing a number of species occurring in different habitats from agricultural landscapes to various types of forests all over Europe, local explanations, such as habitat fragmentation, are insufficient (Hörnfeldt *et al.* 2006). Climate change, on the other hand, is undoubtedly affecting most animal populations in Europe, and will almost certainly have an impact on animal population dynamics.

Many researchers have suggested that mild and unstable winters are detrimental to the overwinter survival of small rodents, and are causing persistently low spring densities and dampened cyclicity (Aars and Ims 2002, Bierman *et al.* 2006, Korslund and Steen 2006, Kausrud *et al.* 2008). This notion originates from the work of Hansson & Henttonen (Hansson and Henttonen 1985, Hansson 1987), describing a latitudinal gradient of cyclicity in Fennoscandian vole populations, and implicating the depth and duration of snow cover as a key factor shaping the interactions between voles and the specialist and generalist predators. During winter, voles occupy the well-insulated subnivean space, where temperature is stable and voles are relatively well protected from all but the smallest predators – only the small mustelids have easy access to the subnivean space. Long and snowy winters in the north are thought to set the stage for a strong interaction between voles and the specialist predators, which would cause weak direct and strong delayed density dependence, and consequently strong and long multiannual cycles. Towards the south, the impact of the generalist and avian predators increases, due to reduced duration and depth of the snow cover, dampening and shortening the cycle. More recently, vole population densities have been suggested to decline when winter temperatures increase and hover around 0°C, causing conditions in the sub-nivean space to deteriorate (Aars and Ims 2002, Korslund and Steen 2006, Kausrud et al. 2008). This would cause repeated winter declines and low

spring densities, inhibit the increase phase of the cycle and cause seasonal population dynamics. However, multiannual cycles exist in regions with relatively mild winters (Salamolard *et al.* 2000, Tkadlec and Stenseth 2001, Lambin *et al.* 2006, Brommer *et al.* 2010, Zub *et al.* 2012), so the role of winter climate in determining vole population dynamics is not clear. So far, little attention has been paid to the impact of changing growing season conditions, although the length of the breeding season is often identified as an important factor (Stenseth *et al.* 1998, Tkadlec and Stenseth 2001, Taylor *et al.* 2013).

1.6 Theory synthesis

To summarize, the boreal vole cycle is currently thought to arise from the interaction between voles and the specialist predators, but not without the influence of the generalist mammalian predators, avian predators, and intra-specific and food-mediated factors. The cessation of the increase phase and initiation of the decline is probably caused by multiple synergistic mechanisms. The dramatic crash phase is most plausibly caused by predators, of which the small mustelids, whose population density reaches its peak during the decline phase or the cycle, have the ability to reduce the density of voles to an extremely low level. While the generalist predators switch to alternative prey, and the avian predators may migrate or refrain from breeding, the small mustelids continue to prey on voles until the vole density is too low to support them. The sparse vole population now faces very little predation and competition, and eventually begins to increase again. Climatic warming is thought to interfere with the above-detailed pattern by reducing the protective snow cover, causing ice-formation on the ground, and exposing voles and the small mustelids to harsh environmental conditions and generalist predators, thus inhibiting the cyclic increase in population density. However, the evidence for this is sporadic. Furthermore, no data exist as to how the predator-vole interactions, which are thought to be the driving force of the Fennoscandian vole cycle, are influenced by the abiotic environment.

1.7 Aims and scope

The objectives of my PhD thesis are 1) to characterize the spatiotemporal variation in vole population dynamics, and in the interactions between voles and the different predator groups in Finland, 2) to investigate the climate-dependence of the phenomena, and 3) to build a model, which will predict vole and predator population dynamics in different climate scenarios.

First I will address the suspected collapse of the vole cycle in Finland and investigate the extent and quality of the changes in the vole cycle since 1980. I will correlate the observed variation in vole population dynamics with

variation in climate to assess whether climate determines the type of vole population dynamics. I will identify climatic factors most strongly associated with the type of vole population dynamics, and specifically, test the hypothesis that warming winters are resulting in dampening small rodent cycles in the boreal ecosystem.

Next, I will characterize the geographic and temporal variation in predator-vole interactions. I will estimate the time lags in the responses of different predator groups to vole densities as well as the effects of predators on vole population growth rates. Furthermore, I will use the data-derived parameter estimates to simulate vole population dynamics under a number of scenarios to gauge the roles of different predators in the boreal vole cycle.

Finally, I will combine the data on vole abundance, predator abundance, and climate to build a climate-based model of vole and predator population dynamics. Given a climate scenario, the model should be able to predict how the vole and predator populations will interact, and what kind of population dynamics results from these interactions. This model will be used to predict how vole and predator populations in northern Europe will respond to climate change.

2   MATERIALS AND METHODS

2.1   Animal and climate monitoring data

The work is based on long-term monitoring data of animal populations and climate. Vole populations have been monitored with snap trapping for several decades by the Finnish Forest Research Institute (Metla), and by researchers of the universities of Helsinki and Turku. The vole data consist of >25 000 vole observations collected in spring and autumn at 32 trapping sites located throughout Finland, mostly since the 1970s (Fig. 5). The data include all vole species of the genera *Microtus* and *Myodes*. A decision was made to pool the vole species instead of investigating the different species separately, because the different species fluctuate in synchrony (Henttonen *et al.* 1977, Hansson and Henttonen 1988, Huitu *et al.* 2004, Korpimäki *et al.* 2005), and the aim was to investigate large-scale patterns in vole community dynamics and in the interactions between the vole and the predator communities.

Data on the abundances of mammalian predators were acquired from the wildlife triangle scheme of the Finnish Game and Fisheries Research Institute, based on snow track counts (Lindén *et al.* 1996). Abundances of the generalist mammalian predators, the red fox (*Vulpes vulpes*), and the pine marten (*Martes martes*), as well as abundances of the specialist small mustelids, the least weasel (*Mustela nivalis*) and the stoat (*Mustela erminea*) were included in the analyses. The indices of the red fox and the pine marten were combined to form an index of generalist mammalian predators, and the indices of the least weasel and the stoat were combined into an index of specialist mammalian predators. The least weasel is more specialized on voles than the stoat and the two species may vary in their interactions with voles (Korpimäki *et al.* 1991). However, it was not known how well the species are distinguished in the snow track data, and whether the accuracy of species identification is stable temporally and spatially. Furthermore, including two variables with potentially highly overlapping information would have complicated the interpretation of the results. With respect to the generalist predators, there was little reason to expect great

differences in their interactions with voles, so for simplicity, their indices were combined, as well.

Abundances of avian predators have been monitored with the Raptor Questionnaire, organized by the Finnish Museum of Natural History (Saurola 2008). Data on the numbers of nesting pairs and the numbers of chicks for 11 vole-eating avian predator species (the short-eared owl *Asio flammeus,* the long-eared owl *Asio otus,* Tengmalm's owl *Aegolius funereus,* the pygmy owl *Glaucidium passerinum,* the Eurasian kestrel *Falco tinnunculus*, the hen harrier *Circus cyaneus*, the rough-legged buzzard *Buteo lagopus,* the Ural owl *Strix uralensis,* the tawny owl *Strix aluco,* the eagle owl *Bubo bubo,* and the common buzzard *Buteo buteo*) were obtained from the database. The abundances of the avian predator species correlated strongly, and were therefore combined to form an avian predator index. The predator density indices at the vole trapping locations were spatially interpolated using inverse distance-weighted averaging (mammalian predators) or averaging over all nearby monitoring regions (avian predators) to accommodate regression analyses with the vole time series.

Daily weather data, interpolated for the vole trapping locations, were obtained from the Finnish Meteorological Institute (Venäläinen *et al.* 2005).

It should be noted, that due to the observational nature of the data, the analyses are largely restricted to pattern description. Proximate mechanisms behind the observed associations may be hypothesized based on available literature, but overall, there is very little scope for inference of causality. The climatic associations are extremely complex and may arise via multiple ecological mechanisms; I present some potential links but attempt to refrain from excessive speculation. Although the abundance of alternative prey, or the quality and quantity of food plants were not measured, they are likely to be highly correlated with climate and therefore implicitly included in the analyses, and may contribute to the climate-dependence of predator-vole interactions.
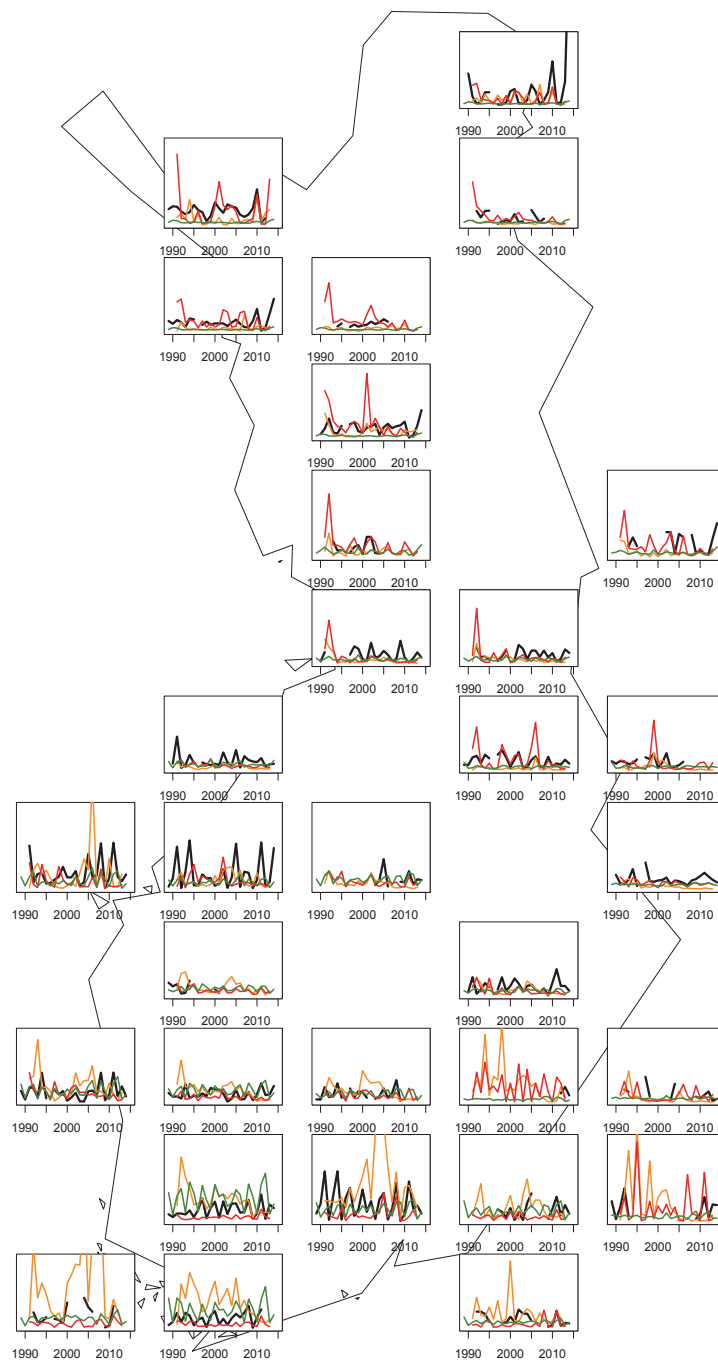
23

FIGURE 5   Vole (black) and predator (red = small mustelids, orange = generalist mammalian predators, green = avian predators) density time series 1989–2011 (II). The locations of the time series on the map correspond very roughly to the location of the vole-trapping site (NB, all trapping sites are in reality within the borders of mainland-Finland).

2.2 Statistical analyses

2.2.1 General considerations

Seasonal vole population growth rates and predator population indices were modelled using log-linear autoregressive models (Royama 1992, Stenseth 1999). Wavelet analysis, often used to identify periodicity in ecological time series (Cazelles *et al.* 2008) was not employed, as it does not directly assess density dependence. Another potentially useful approach not used here, is to allow for phase-dependence of the density dependence parameters (e.g. Framstad *et al.* 1997). There was some evidence of phase-dependence in the vole population growth rates during winter (Fig. 6a, b), but not during summer (Fig. 6c, d). As the goal was to estimate the spatial, temporal, and climatic variation of density dependence, estimating all of these in a phase-dependent manner would have made the models and their interpretation very complicated.

In terms of predator-prey models, there is a rich literature of mechanistic models applied to the question of vole-weasel interactions (e.g. Hanski *et al.* 1991, Hanski and Korpimäki 1995, Hanski and Henttonen 1996, Turchin and Hanski 1997, Oksanen *et al.* 2001, Turchin and Ellner 2000, Hanski *et al.* 2001, Turchin and Hanski 2001, Hanski and Henttonen 2002). Mechanistic models have the benefit of explicitly inferring a biological understanding of the process (Kendall *et al.* 1999). However, in order to use a mechanistic model for prediction, one would need to predict the future values of all relevant biological parameters, such as carrying capacities, intrinsic population growth rates and mortality rates, numeric and functional responses of predators, and intraspecific competition and territoriality. This is not possible with the currently available data. Therefore, a phenomenological model, which does not necessitate a deteailed *a priori* hypothesis of the underlying biological mechanisms, is better suited for the task at hand, given the available data. Furthermore, there is a distinct paucity of phenomenological predator-vole models in the literature, due to the lack of predator time series.

All analyses were conducted in R (R Core Team 2012), using the libraries nlme (Pinheiro *et al.* 2013), MASS (Venables and Ripley 2002), gstat (Pebesma 2004), maptools (Lewin-Koh *et al.* 2011), and qgraph (Epskamp *et al.* 2012). Generalized least squares (GLS) models were used to model the spatial autocorrelation or climate-associated variance of the residuals. Akaike Information Criterion (AIC) -based model selection was used to determine the best model structure. All models were validated by dividing the data set randomly into a training set (50% of the data points) and a test set (50%), refitting the models to the training data, and using these models to predict the test data. Also, the parameter estimates from the models were used to simulate vole (and predator) population dynamics, and the resulting simulated population time series were compared to the observed time series; all models, which failed to recreate the observed dynamics, were rejected.
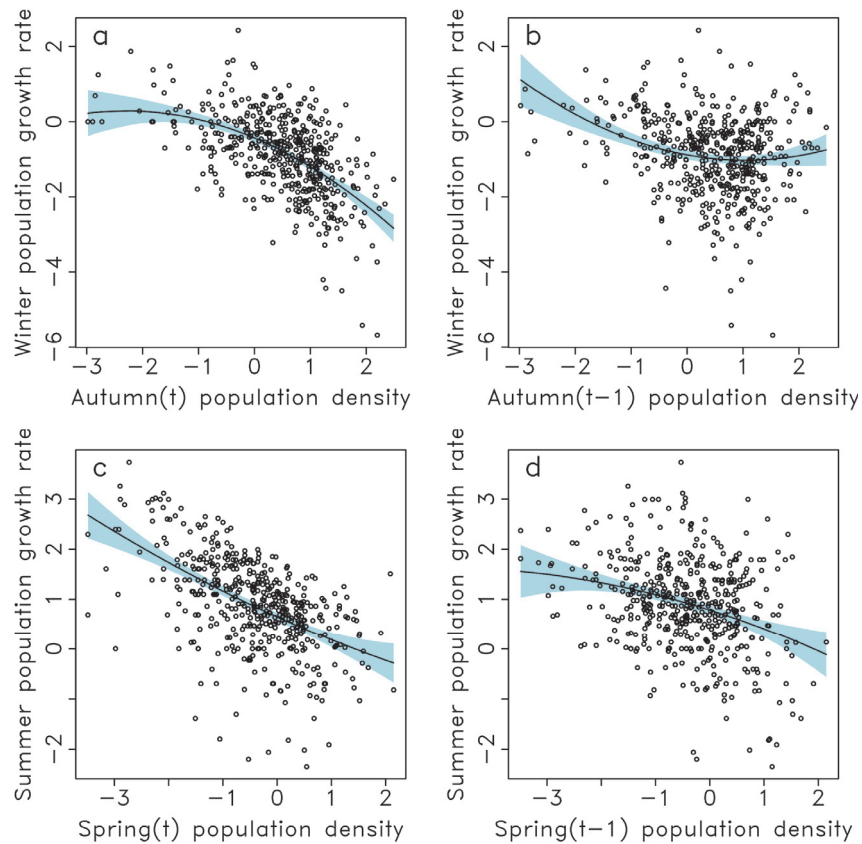
25

FIGURE 6   Density dependence of vole population growth rate during winter (a, b) and summer (c, d) (I). The black lines are shaded areas show the fit of a linear model (predicted mean value ± 95% confidence intervals).

2.2.2 Spatiotemporal variation in vole population dynamics (I)

To identify the spatial and temporal variation in vole population dynamics, the direct and the delayed density dependence of vole population growth rate were estimated from the data for each year and each population. Instead of treating all 32 time-series independently, a single model was fitted to the whole data set, allowing for spatial and temporal variation in population growth rates and in density dependence. Because the ecological mechanism behind density dependence is likely to vary between the seasons, winter and summer population growth rates were modelled separately.

First, the basic structure of density dependence was determined by assessing which previously measured population densities should be included in the models. Using the defined density dependence structure, the spatial and temporal variation in density dependence was estimated by fitting to the data a model, which allowed the parameters to vary geographically and temporally. The temporal variation was expected to be potentially nonlinear, as climate and possibly other environmental conditions have fluctuated during the study

period in a nonlinear manner. Further, the temporal variation was expected to vary geographically. However, to keep the model as simple as possible, the geographic variation was expected to be linear, akin to the latitudinal and longitudinal climatic gradients.

2.2.3 Influence of climate on vole population dynamics (I)

The next question was, whether the observed temporal and geographic variation in vole population dynamics could be attributed to variation in climate. If the variation in vole population dynamics was caused by variation in climate, replacing the geographic coordinates and time with the right climatic covariates should improve model fit. The key was to find the best climatic covariates for each parameter in the seasonal population growth rate models. Large-scale climatic indices, such as the North Atlantic Oscillation (NAO), have been advocated as better predictors of ecological phenomena than local climate variables (Ottersen *et al.* 2001, Hallett *et al.* 2004). However, when the aim is to understand both geographic and temporal patterns related to climate, information on local climate is necessary. Different combinations of weather variables were tested as covariates for each parameter, and compared with AIC to models with latitude, longitude, and year as the covariates.

2.2.4 Geographic and temporal variation in predator-vole interactions (II)

To estimate the spatial and temporal variation in the predator-vole interactions, seasonal vole population growth rates were modelled as a function of vole and predator population indices, and the predator indices were modelled as a function of vole indices:

$S_t - A_{t-1} = a_1 + b_1 A_{t-1} + c_1 A_{t-2} + d_1 P_{1,t} + e_1 P_{2,t} + f_1 P_{3,t-1} + \varepsilon_{1,t}$ (Model 1)
$A_t - S_t = a_2 + b_2 S_t + c_2 S_{t-1} + d_2 P_{1,t} + e_2 P_{2,t} + f_2 P_{3,t} + \varepsilon_{2,t}$ (Model 2)
$P_{1,t} = a_3 + g_1 A_{t-1} + h_1 S_{t-1} + i_1 A_{t-2} + \varepsilon_{3,t}$, (Model 3)
$P_{2,t} = a_4 + g_2 A_{t-1} + h_2 S_{t-1} + i_2 A_{t-2} + \varepsilon_{4,t}$, (Model 4)
$P_{3,t} = a_5 + g_3 S_t + h_3 A_{t-1} + i_3 S_{t-1} + \varepsilon_{5,t}$ (Model 5)

S represents the spring density of voles, A the autumn density of voles, P_1 the winter density of the small mustelids, P_2 the winter density of the generalist mammalian predators, and P_3 the summer density of the avian predators. ε represents the residuals, which were normally distributed and homoscedastic based on visual observations. The parameters *a-i* were allowed to vary geographically and temporally. In addition to the above-specified model, various biologically relevant model structures were initially tested, including inter-predator interactions and density-dependent predation (vole density-predator interactions). These however failed to produce meaningful population dynamics in simulations and were therefore discarded as faulty. It may not be possible to accurately estimate such subtle phenomena based on the large-scale monitoring data.

To assess the roles of the different predator groups in the vole cycle in different regions, parameter estimates for the year 2011 and for three regions (northern, eastern, and western Finland) were used to simulate vole population dynamics in different predation scenarios. In each scenario, the densities of certain predator groups were set to the minimum observed value, in order to simulate their absence from the ecosystem.

2.2.5 Influence of climate on predator-vole interactions (III)

To construct a climate-based model for predator-vole interactions, climatic covariates for all parameters in Models 1-5 were determined by AIC-based model selection. The performance of the climate-based models was validated by a comparison to the spatio-temporally varying models, and by comparing the model predictions to the observed population dynamics.

2.2.6 Predicting vole population dynamics under climate change (IV)

The climate-based predator-vole models (III) were used to predict vole population dynamics under different climate scenarios, both observed and predicted. The performance of the models was confirmed by recreating past population dynamics in Finland and in Sweden (independent climate data, not used to parameterize the model), based solely on observed climate. Because the model successfully recreated the observed geographic and temporal variation in vole population dynamics, the model was then used to predict vole population dynamics under expected future climate scenarios over the next decades (2011–2039). Predicting further into future would not be meaningful for several reasons. First, the climate predictions based on the different greenhouse gas emission scenarios begin to diverge rapidly at 2040, adding a considerable amount of uncertainty. Second, the vole-predator models cannot be expected to function in climatic and biotic environments that are very different from the training data, i.e. data from Finland 1989–2011. As the climate changes, the structure of ecosystems in Fennoscandia will eventually change, as well, and the models based on the current climatic range and the current species composition will no longer be relevant.

2.2.7 Geographic synchrony of vole population fluctuations

To test which factor, predation or climate, better accounts for the geographic synchrony (i.e. the spatial autocorrelation of vole population growth rates), different variants of the seasonal vole population growth rate models were compared with AIC to models with spatially auto-correlated residual structure. If the performance of a model is improved by modeling the residuals as spatially auto-correlated, the terms in the model do not account for the geographic synchrony. The performance of different model structures, including or excluding the different predator groups and climate, were tested with and without spatially auto-correlated residual structure.

3   RESULTS AND DISCUSSION

3.1   The boreal vole cycle has not disappeared

A range of different types of temporal changes was evident in the population dynamics of voles in Finland: some populations did shift from cyclic to seasonal dynamics; others appeared to gain a regular cycle; some showed consistently cyclic dynamics with no clear temporal changes; while others exhibited irregular dynamics throughout the study period (I). Certainly not all vole populations shifted to irregular or low-amplitude fluctuations, and most intriguingly, those that did, are located in the coldest and snowiest regions of Finland, the north and the east (I). The results contradict the claim that a Europe-wide dampening of cyclicity is occurring (Cornulier *et al.* 2013), and that warming winters are the cause (Aars and Ims 2002, Bierman *et al.* 2006, Korslund and Steen 2006). Strann et al. (2002), studying vole population dynamics in northern Norway, reached the same conclusion. Furthermore, reduced spring densities have been identified as a general characteristic of the pan-European dampening of cyclicity (Cornulier *et al.* 2013), but in Finland, the spring densities of vole populations have not consistently declined (Fig. 7). This further contradicts the idea of a continental-scale syndrome of dampening vole cycles.

The northern high-amplitude cycle collapsed in the early 1980s, due to a dramatic weakening of delayed density dependence (Fig. 8). Since the mid-1990s, delayed density dependence has been slowly regaining its strength, and appears to have now restored the vole cycle in northern Finland (Fig. 8). The loss and return of the cycle in the north occurred without corresponding changes in winter snow depth (I). Similarly, the vole cycle in eastern Finland is on the verge of collapse (Fig. 8), although winters remain very snowy (I). Vole populations in the southwest, with mild and unpredictable winters and declining snow cover, showed no sings of weakening cyclicity (Fig. 8). The difference between eastern and western Finland was caused by opposing temporal trends in delayed density dependence during summers (Fig. 9a). The

cycle is maintained in the west by the strengthening delayed density dependence during summers (Fig. 9a), while delayed density dependence during winters is weakening in both regions (Fig. 9b).

Because of the geographically varying changes in vole population dynamics, the Fennoscandian latitudinal gradient in cyclicity disappeared as the northern cycle collapsed (Fig. 8). Indeed, Stenseth (1999) predicted that the gradient might turn out more complicated than expected, Strann *et al.* (2002) showed that the latitudinal gradient does not apply to all Fennoscandian vole populations, and Henden *et al.* (2009) reported that geographic gradients in cyclicity in Norway have varied in time. It appears that the Fennoscandian cyclicity gradient, a deeply rooted concept, is not as robust and static as is often thought. Evidently, a latitudinal climatic gradient may not be a good proxy for temporal climate change. General conclusions should not be drawn from data collected over a short time period along geographic gradients; temporal variation is necessary for the estimation of ecological responses to local changes.
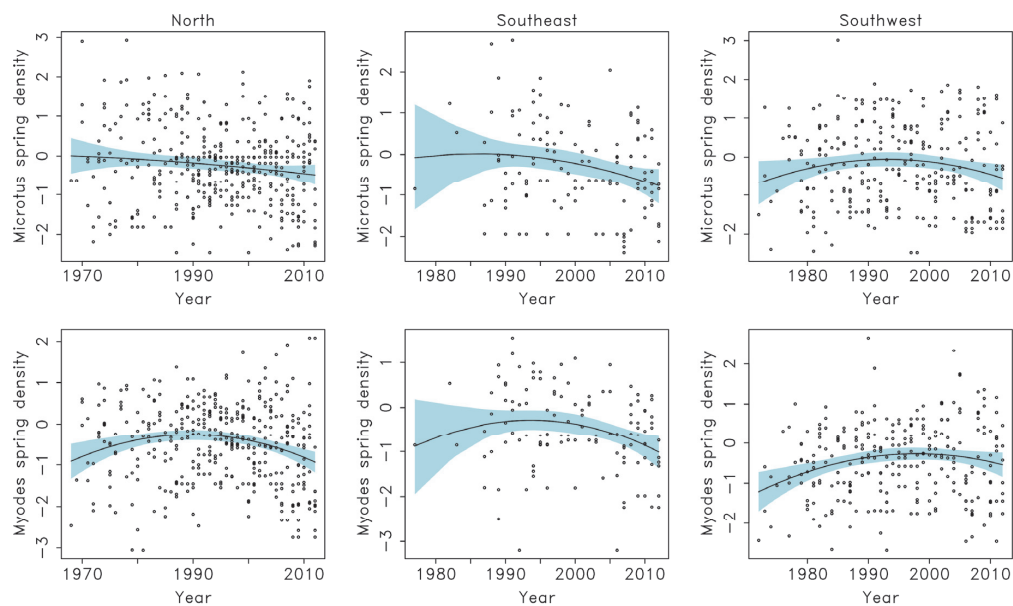
FIGURE 7   Temporal trends in the spring densities of vole populations in different regions in Finland (I): north (64–70°N and 20–30°E), southeast (60–64°N and 26–33°E), and southwest (60–64°N and 20–26°E). The black lines and shaded areas show the fit of a linear model (predicted mean value ± 95% confidence intervals).

FIGURE 8   Temporal trends in the annual density dependence of vole population growth
            rates in different locations in Finland (north: 68°N 25°E; southwest: 62°N
            23°N; southeast: 62°N 29°N), calculated based on seasonal vole population
            growth rate models (I).

FIGURE 9   Temporal trends in the density dependence of summer (a) and winter (b)
            population growth rates of voles (I).

3.2 Predation may explain the changes in vole dynamics

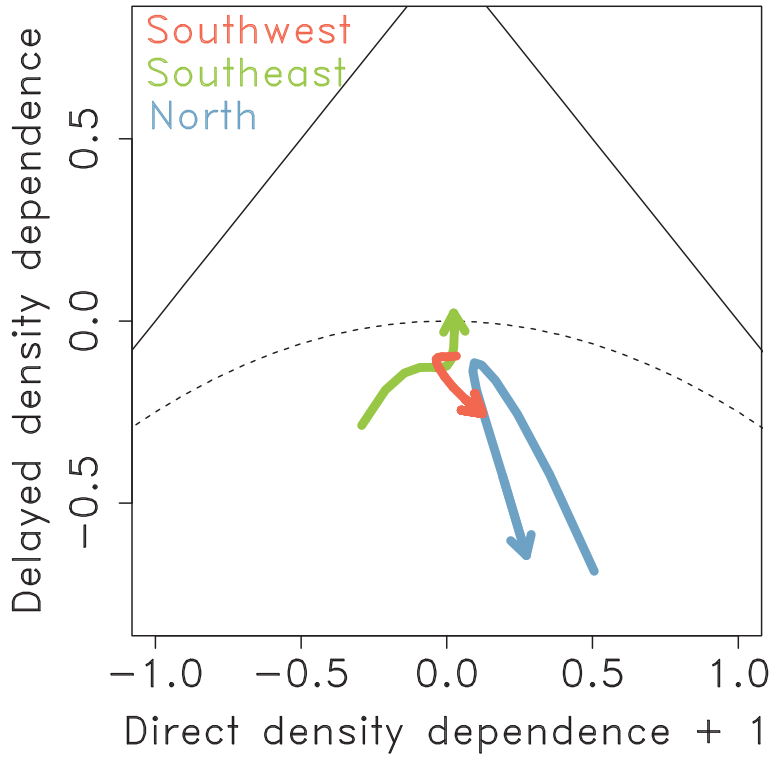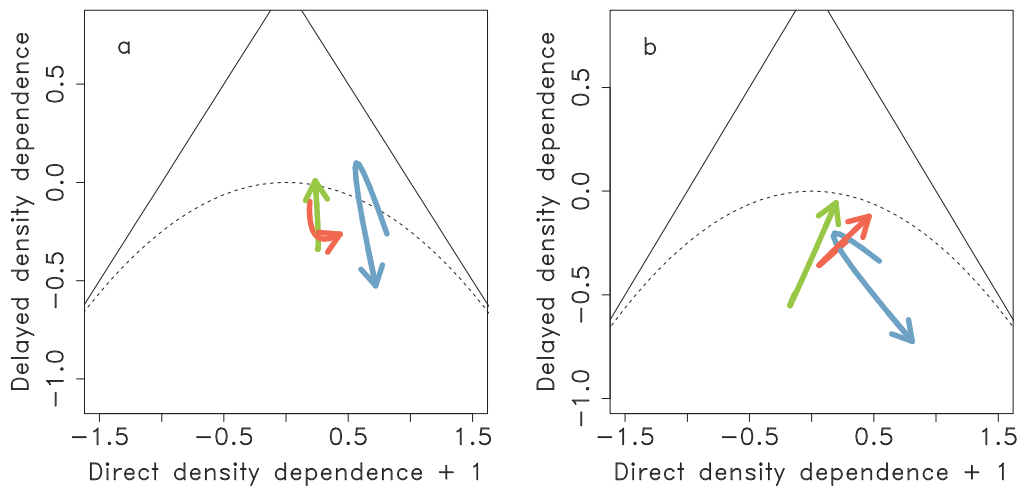The population densities of *Microtus* and *Myodes* voles fluctuated in synchrony in all regions (I). The intra-generic delayed density dependence, estimated separately for each genus, corresponded to the community-level density dependence (I), strongly supporting the notion that the boreal vole cycle is a community phenomenon (Hansson and Henttonen 1988, Huitu *et al.* 2004, Korpimäki *et al.* 2005). Therefore, the mechanism behind the observed variation in vole population dynamics must be applicable to both vole genera. Intraspecific and genus-specific mechanisms, such as variation in life-history traits or food plants are unlikely, as they are not shared by the two genera. The main ecological force shared by *Microtus* and *Myodes* voles is predation.

The predator exclusion simulations further underscored the importance of predation in vole population dynamics (II). The exclusion of the small mustelids in western Finland, and of the small mustelids and avian predators in northern Finland, resulted in the loss of regular multiannual cyclicity, strongly suggesting that these predator groups play a major role in the cycle and that changes in predation can have dramatic consequences on the dynamics of the prey populations (II). In eastern Finland, where vole populations are no longer clearly cyclic (I), the simulated predator exclusion did not alter vole population dynamics, which indicates that predation in this region is no longer a source of delayed density dependence (II).

Most importantly, the observed alterations in the delayed density dependence of vole population growth rates, and of vole population dynamics, coincided with changing interactions between voles and the small mustelids. During the non-cyclic period in northern Finland, the influence of the small mustelids on vole population growth rates was estimated to be extremely weak (II, IV). Simultaneously with the recent return of the cycle, the influence of the small mustelids strengthened (II, IV). The weak influence of the small mustelids may have been caused by a decrease in the relative abundance of the least weasel (II), the more specialized small mustelid. The least weasel was abundant in the north before the decline of the cycle, when the stoat became dominant (Henttonen *et al.* 1987), and has increased in abundance over the recent years as the cycle has been restored (II). It is also possible that the least weasel is dependent on vole peaks and can therefore attain high densities only if vole populations are cyclic.

The difference in vole population dynamics between western and eastern Finland was at least partly attributable to the influence of the small mustelids on the summer population growth rates of voles. A crucial factor in the boreal vole cycle appears to be the summer declines in vole density, caused by delayed-density-dependent predation by the small mustelids, especially the least weasel (II). The impact of the small mustelids during summers has increased in the west, where the least weasel is more abundant than the stoat, strengthening the delayed density dependence. The opposite has occurred in

the east, where the two species are roughly equally abundant (II). A further difference between the predator communities in eastern and western Finland is the relative abundance of the red fox, which is more dependent on voles than the pine marten, a true generalist (Lindström 1983, Lindström 1988, Helldin 1999). The red fox population has declined in eastern Finland over the last decades due to an increase in lynx density (Elmhagen *et al.* 2010).

The interactions between predators and voles varied widely in different climates (III). The magnitude and time lag in the predators' responses to vole population densities, as well as the timing and strength of their influence on vole population growth rates were dependent on climate (III). Predators are often categorized strictly into specialists and generalists, and the influence of predation on prey population dynamics is then inferred from the assumed functional response of each predator type. However, the degree of specialization of the predators may vary depending on environmental conditions (II, III). A predator species may act as a specialist in certain environments, and as a generalist in others. This was especially clear for the "generalist" predators, the red fox and the pine marten, which appeared to fill the role of cycle-dampening generalists only in relatively warm climatic conditions, interacting with voles in a delayed-density-dependent manner in cold climates (III). Similarly, the avian predators were predicted to contribute to delayed density dependence only in climates with relatively warm summers and high precipitation (III).

Although intra-guild predation was not explicitly modelled, it is likely to be implicitly contained in the parameter estimates: an estimated positivite effect of the avian and the generalist mammalian predators on vole population growth rates likely reflects at least partly the impact of intra-guild predation on the small mustelids. With this assumption, the results suggest that intra-guild predation on the small mustelids is mainly exerted by the avian predators during summers. This appeared to occur mostly in climates with cold winters, potentially reflecting the paucity of alternative prey. According to Oksanen *et al.* (2001), the cycle-stabilizing effect of the generalist and avian predators in southern Fennoscandia is caused by their impact on the small mustelids, rather than their direct effect on the vole populations. My results did not support this argument, as the generalist and avian predators were estimated to have the strongest direct negative effects on vole populations in warm climates.

Overall, the results largely concur with the conclusions of earlier mechanistic models and empirical observations, suggesting that the interaction between predators, especially the small mustelids, and voles is the driving force of the Fennoscandian vole cycle. The fact that such different approaches, based on different types of data and models, all lead to the same conclusion is strong support for the predation hypothesis.

3.3 Mild winters do not cause dampening cyclicity

Winter weather did not have a consistent effect on the winter population growth rate of voles (I, III). No strong associations between the animal populations and snow depth were found (Fig. 10). Contrary to expectations, mild winters were not associated with strong generalist and avian predation and weak specialist predator influence on vole populations (III). It is worth noting, however, that winters in Finland are much colder and longer than winters in regions where reduced vole survival or reduced cyclicity has been associated with winter weather, e.g. southern Norway (Aars and Ims 2002, Kausrud *et al.* 2008) and northern England (Bierman *et al.* 2006). Even at the southwestern coast of Finland, there is on average one mid-winter (December to February) day every four years, when the mean temperature is above 0°C. Anecdotally, the winter of 2013–2014 was exceptionally warm (>2°C warmer than the average during 1981–2000, http://ilmatieteenlaitos.fi/talvitilanne) with very little snow. In southern Finland, there was practically no snow cover, and although the average temperature was warm, temperatures below -30°C occurred occasionally. Vole populations were initiating a cyclic increase in summer 2013 but declined considerably during the winter. Such extreme weather conditions, which did not occur during the study period (1970–2011), and which are not predicted become the norm in the near future (Jylhä *et al.* 2009, Kellomäki *et al.* 2010), may resemble the conditions observed in the Norwegian and British studies.

Although the vole cycle was not dependent on winter conditions, winter weather did influence the interaction between voles and the specialist predators. The small mustelids were estimated to cause strongly negative delayed density dependence during winters only in cold climates, as observed in northern Finland e.g. by Hansen *et al.* (1999). The delayed density dependence of vole population growth rate during winter was associated with mid-winter snow depth (I), and the abundance of the small mustelids was associated with precipitation during mid-winter (III). This suggests that a strong interaction between voles and the small mustelids during winter is dependent on snow conditions, possibly as described by Kausrud *et al.* (2008) for lemmings. However, increasing precipitation was predicted to strengthen the influence of the small mustelids, and consequently the delayed density dependence, during summers (III), enabling cyclic population dynamics irrespective of winter conditions. The increase in precipitation over the last decades is thus likely to explain the observations of strengthening delayed density dependence (I) and small mustelid predation (II) during summers in western and northern Finland. The mechanism through which changes in precipitation translate to changes in predator-vole interactions cannot be identified with the current data and deserves further investigation.

Growing season conditions appeared important for vole population dynamics (I) and predator-vole interactions (III). Warm summers were

34

associated with high avian predator abundances and strong impact of the avian and generalist predators on vole population growth rates during winter (III) and thereby with strong direct density dependence during winter (I). The southward reduction in cycle period is thus likely to arise from a gradient of increasing growing season temperatures, which, possibly via increased overall abundance of various prey species, increases the reproductive success and the population size of overwintering avian predators, especially if the autumn vole population density is high.
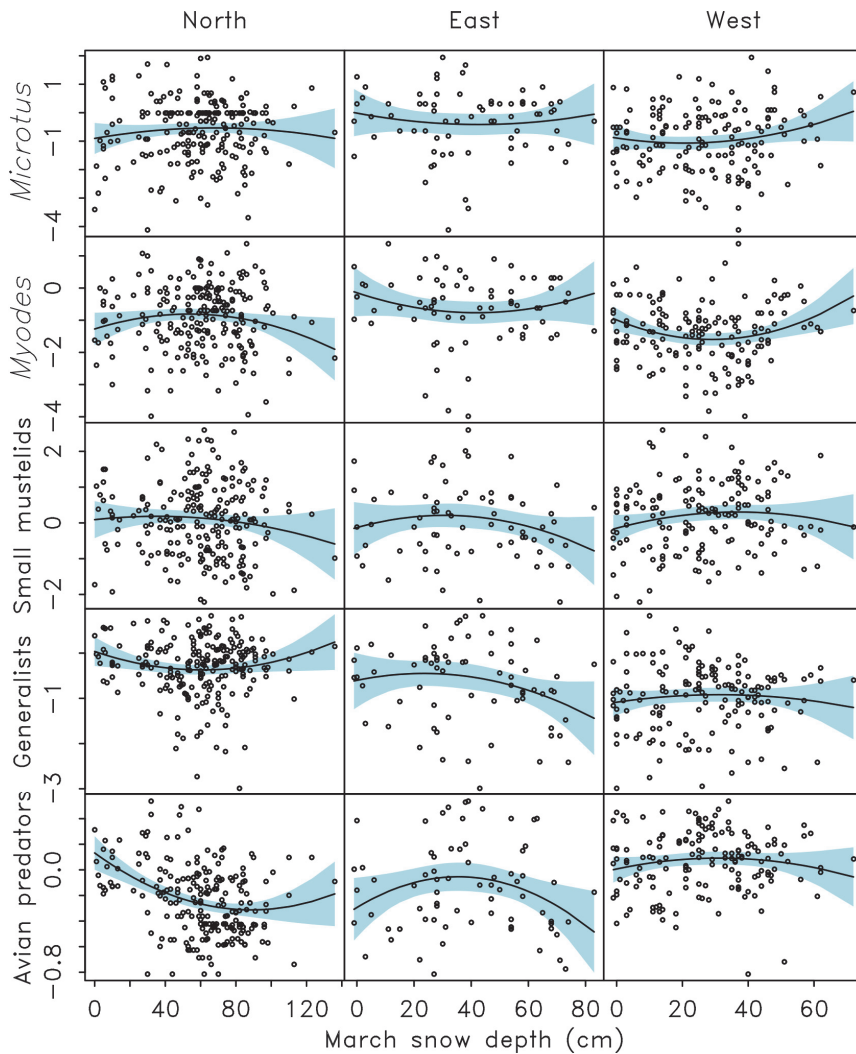
FIGURE 10   Associations between animal population indices (vole population growth rates during winter and predator density indices) and average snow depth in March (representing the accumulation of snow over the winter season) (I). North (64–70°N and 20–30°E), southeast (60–64°N and 26–33°E), and southwest (60–64°N and 20–26°E). The black lines are shaded areas show the fit of a linear model (predicted value ± 95% confidence intervals).

To summarize, in very cold conditions, the interaction between voles and the small mustelids during winters created strongly negative delayed density dependence and high-amplitude, long cycles (III, IV). Under relatively warm and humid conditions, the small mustelid-vole interaction during summers, possibly in combination with avian predation during winters, produced somewhat shorter cycles with lower amplitude (II, III, IV). Such conditions prevail e.g. in Poland, where Jedrzejewski *et al.* (1995) noted that small mustelid predation was strongest during summer and autumn. The model predicted that small mustelid-driven vole cycles should not occur in climates with mild-to-warm temperatures and low precipitation. In such climates, the ability of the small mustelids to inhibit vole population growth may be weak, or the small mustelids may subsist partly on other food sources. The proximate mechanism in the former case may be caused e.g. by food-limitation being a stronger regulating factor than predation, and in the latter e.g. by the stoat being more abundant than the least weasel.

3.4   Geographic synchrony

In addition to shaping the vole cycle locally, the data suggest that the avian predators contribute to the large-scale geographic synchrony in vole population dynamics, as shown earlier by Ims and Andreassen (2000) in Norway. The models for the seasonal population growth rates of voles, which included both climate and the predators, were not improved by modeling the residuals as spatially auto-correlated (Table 1), suggesting that the variables in the model, either climate or predators, account for the geographic synchrony. The predator-vole models without climatic information were markedly improved by modeling the residuals as spatially auto-correlated, indicating that weather conditions contribute to the geographic synchrony (the so-called Moran effect, Moran 1953). However, climate alone did not account for all spatial autocorrelation of vole population growth rates. When models with one or all predator groups excluded were compared, the models were improved by including the spatial autocorrelation. The improvement was especially marked for the summer population growth rate model excluding the avian predators, suggesting that particularly during summers, the avian predators play an important role in generating geographic synchrony in vole population fluctuations. During winter, all predators appeared to contribute to the geographic synchrony, although not as much as climate.

TABLE 1   AIC-based comparison of winter and summer vole population growth rate models with different spatial autocorrelation structures. The AIC values of the model variants with different residual structures are compared the models assuming no residual structure, the AIC values of which are set to 0. Low AIC values indicate better model fit.

Fixed terms	Spatial correlation of residuals	Winter	Summer
Climate + predators	No	0.0	0.0
Climate + predators	Exponential	1.1	-0.6
Climate + predators	Linear	-0.3	-0.9
Climate + predators	Gaussian	-0.1	-1.1
Climate + avian + generalist	No	0.0	0.0
Climate + avian + generalist	Exponential	-1.0	-2.0
Climate + avian + generalist	Linear	-2.1	-1.2
Climate + avian + generalist	Gaussian	-2.1	-2.3
Climate + avian + specialist	No	0.0	0.0
Climate + avian + specialist	Exponential	0.0	-2.0
Climate + avian + specialist	Linear	-1.5	-1.8
Climate + avian + specialist	Gaussian	-1.4	-2.7
Climate + mammalian	No	0.0	0.0
Climate + mammalian	Exponential	0.4	-7.1
Climate + mammalian	Linear	-1.6	-8.9
Climate + mammalian	Gaussian	-1.4	-7.6
Climate	No	0.0	0.0
Climate	Exponential	-2.8	-9.9
Climate	Linear	-5.5	-11.2
Climate	Gaussian	-5.4	-10.1
Predators	No	0.0	0.0
Predators	Exponential	-16.2	-25.4
Predators	Linear	-7.0	-14.1
Predators	Gaussian	-7.1	-14.4

3.5 Future of the boreal vole cycle

The climate-based predator-vole interaction model (III) successfully recreated the observed patterns in vole population dynamics, based on observed climate (IV, Fig. 11). Notably, the model even predicted the most recent vole peak in northern Finland in 2011, based on observed climate (vole data for the north were available up to 2009). Thus the variation in vole population dynamics can be explained by variation in climate. Local factors, such as landscape structure

(Ecke *et al.* 2010), may influence individual vole populations, but seem to be of minor importance on a large scale. Some, but not all of the changes in vole population dynamics could be directly attributed to changes in predator-vole interactions, particularly with respect to the small mustelids. However, the results do not exclude the impact of other ecological agents, such as disease, food quality and quantity, and inter- and intraspecific behavioural and life history effects, as these were not measured.

Climatic warming is likely to weaken the boreal vole cycle (IV). The northernmost populations are predicted to revert back to the 1990s-type stable, seasonal dynamics, and the years of superabundant voles to gradually become rare and eventually to disappear. Southern regions are predicted to experience more irregular vole dynamics, with alternating periods on regular cyclicity, low-amplitude seasonal dynamics, and occasional extremely high peak abundances.
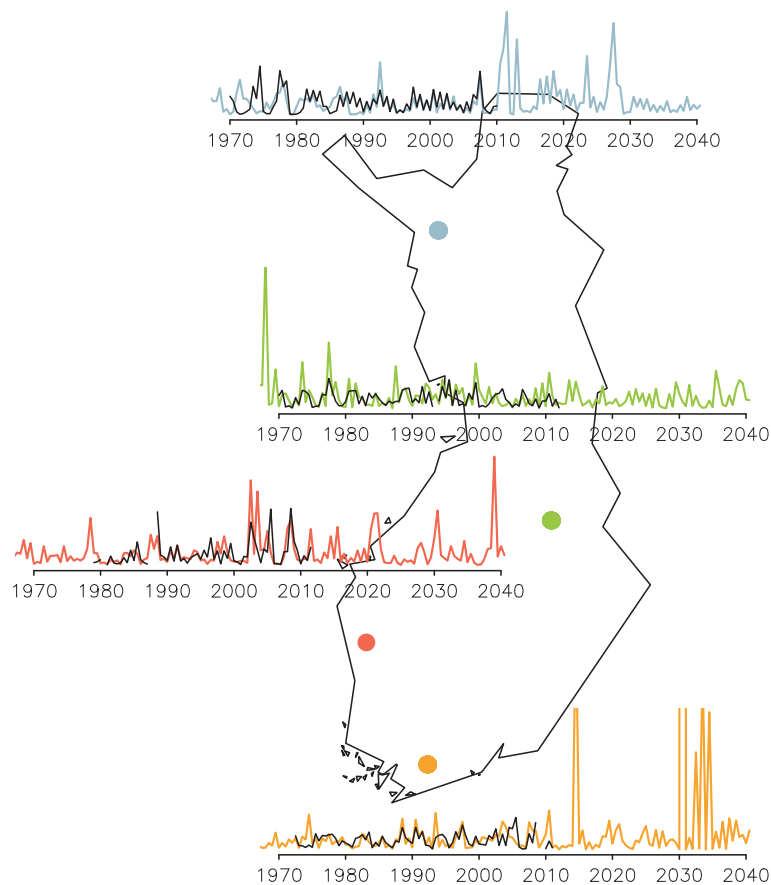

FIGURE 11   Examples of model-predicted vole population dynamics (coloured time series), based on observed climate (up to 2011) and predicted climate (2011–2039) (IV). The black time series are observed vole densities in the given locations.

The potential loss of vole peaks in northern Fennoscandia is alarming because the survival of predator populations, particularly in subarctic regions where alternative prey are relatively scarce, is strongly dependent on the regularly occurring years with high small rodent abundance (Lindström 1988, Sundell *et al.* 2004). The decline of the vole cycle is likely to exacerbate the negative influence of the warming climate on lemming populations (Ims *et al.* 2011). Furthermore, during times of low vole abundance, which is predicted to become the norm, the predation pressure on alternative prey species, such as the mountain hare and forest grouse, both which are declining in numbers (Kauhala and Helle 2007, Ludwig 2007), is strong (Angelstam *et al.* 1984, Reif *et al.* 2001). Hence, in addition to the adverse direct effects of climate change (Ludwig *et al.* 2006, Lehikoinen *et al.* 2009), both predator and prey communities are likely to be affected by the altered vole population dynamics. The changes in vole population dynamics, particularly the presumed decline in spring densities, are thought to endanger populations of avian predators (Hörnfeldt *et al.* 2005, Millon *et al.* 2014). However, in Finland and Sweden, the overall abundance of avian and generalist predators is not predicted to decline, despite the weakening vole cycle (IV). Some species are likely to suffer more than others, and changes in the predator community composition are likely, and may induce further changes in prey populations.

The changing vole population dynamics can be expected influence vegetation patterns, as well. Cyclic vole peaks create an intermittent disturbance regime in plant communities, causing a decline in NDVI (normalized difference vegetation index, from satellite images) values (Olofsson *et al.* 2012) and controlling the composition of plant communities by selectively removing the dominant species (Summerhayes 1941, Howe *et al.* 2006, Rydgren *et al.* 2007). Thus, vole grazing has been shown to increase plant diversity (Summerhayes 1941, Fox 1985, Questad and Foster 2007). Changes in the severity and frequency of vole disturbance may have dramatic consequences on plant communities. The future impact of vole populations on vegetation is likely to differ between southern and northern Fennoscandia, as vole densities are predicted to become increasingly stable in the north (lack of disturbance peaks) and increasingly variable in the south (intermittent, extremely severe disturbance). Overall, a long-term change in the dynamics of a key herbivore group is likely to cascade through the ecosystem, affecting the predator, herbivore, and plant communities, with uncertain consequences.

In all of Fennoscandia, the reduction in the predictability of the vole peaks, together with the emergence of occasional extremely high densities, is worrisome due to the potential for unpredictable crop damage and zoonotic disease risk. In general, changes in the dynamics of pest species are thought to be among the most serious threats to boreal forests (Ayres and Lombardero 2000, Volney and Fleming 2000, Soja *et al.* 2007). Vole damage to forests increases with vole density (Gilbert *et al.* 2013), and the predicted occasional extremely high densities are likely to cause severe destruction of young trees. Currently, vole peaks can be predicted and the damage controlled (Huitu *et al.* 2013), but if vole peaks become unpredictable, mitigation of vole damage

becomes difficult. Furthermore, as the population dynamics of many herbivorous insect species (e.g. *Choristoneura fumiferana*: Royama 1992, and *Epirrita autumnata*: Klemola *et al.* 2002) are thought to be governed by similar ecological principles as the predator-vole cycle, i.e. mortality caused by natural enemies, and to follow similar climatic gradients (Volney and Fleming 2000, Klemola *et al.* 2002), it is possible that insect outbreaks become increasingly unpredictable and severe, as well. The synergistic effects of herbivore damage and drought may increasingly hinder the renewal and growth of forests.

In terms of impact on the human society, rodent populations are an important reservoir of zoonotic diseases, whose incidence follows vole population density (Kallio *et al.* 2009, Rossow *et al.* 2014). Regularly fluctuating rodent densities allow an accurate prediction of disease risk, which is not possible if the rodents shift to irregular dynamics. Furthermore, the predicted increase in amplitude means that zoonotic disease incidence will not only be more difficult to predict, but the risk may increase rapidly to very high levels. The combination of more favorable climatic conditions and increasingly irregular, high-amplitude rodent fluctuations may dramatically alter the zoonotic disease landscape in northern Europe.

3.6 Reliability of the results

3.6.1 Reliability of the animal data

The vole indices can be considered a fairly accurate representation of the vole population densities (Hanski *et al.* 1994). The data were collected in a standardized fashion using snap trapping, and the vole density index correlates with various measures known to depend on vole abundance, such as the incidence of Hantavirus infections in the human population (Kallio *et al.* 2009) and the damage to tree seedlings (Huitu *et al.* 2009).

The predator data, however, are not validated to the same extent. The fact that the model including vole densities and climate explained a mere 50% of the variation in the small mustelid index is suggestive of a significant amount of measurement error in the small mustelid index. In comparison, the model explained 61% of the variation in the generalist predator index, which is expected to be relatively independent of vole densities. In contrast to the larger generalist predators, the small mustelids are able to move under the snow cover where their prey reside. In this light, while the snow track index may be an accurate measure of fox and pine marten abundance, it is inherently inadept at measuring the abundance of the small mustelids due to their largely sub-nivean life-style. Instead of their abundance, the snow track index measures the above-snow activity of the small mustelids, which may or may not be associated with the small mustelid abundance. Various factors, such as high population density or poor food availability may cause increased above-snow dispersal (discussed e.g. in Sundell *et al*. 2013).

What the mammalian predator indices measure is likely to depend on weather conditions; e.g. weather conditions during winter will influence the duration and visibility of the snow tracks, but potentially also the activity of the animals. Indeed, depending on the weather conditions, the snow track index may measure the true abundance of the predator, the above-snow activity of the predator, or the visibility of the tracks. The guidelines set for the snow track counting attempt to minimize the variation in weather conditions, but in the worst case, the estimated climate-dependent variation in the predator-vole interaction may in fact reflect a climate-dependence of the meaning of the predator index.

A further source of error in the predator data set is the spatial interpolation step. As the predator populations were not monitored in the same location as the vole populations, the predator indices at the vole trapping sites had to be interpolated. Interpolation can be done using different models, which have different assumptions about the spatial autocorrelation patterns in the predator data. Inverse distance-weighted interpolation was employed, with the weight decreasing by distance[2], including all data points. Different interpolation methods could have resulted in different estimated predator abundances and thereby different estimated predator-vole interactions. The method was selected based on variograms and model comparison, and comparing the interpolated predator time series with the vole time series.

The uncertainty of what the predator indices actually measure severely hampers the interpretation of the results. The predator indices failed to account for all density dependence in vole population growth rates (II), due to the error in the predator indices, or alternatively, due to other ecological factors contributing to density dependence. With the current data, the reason cannot be resolved. However, this does not prohibit the use of the model in predicting vole population dynamics under different climate scenarios. An index whose meaning varies with climate may be useful, as long as the model allows for the climate-dependence. The model was able to recreate the observed spatiotemporal patterns in cyclicity, indicating that the changes observed in vole population dynamics can be explained by climate and that the model performs adequately despite the imperfections in the training data.

3.6.2 Reliability of the climate data

The climate data have been collected in a standardized way by the Finnish Meteorological Institute at >400 observation stations (Venäläinen *et al.* 2005). Over the decades, automatic measuring and data recording has become increasingly common, but attempts have been made to maintain temporal continuity in the measuring protocol (Venäläinen *et al.* 2005). The precipitation gauge changed in the early 1980s, which caused a small increase in the precipitation measures (Tuomenvirta 2004). Furthermore, precipitation measurements are subject to multiple sources of error (Førland et al. 1996). Venäläinen *et al.* (2009) do not mention of any measures being taken to correct the precipitation data. The climate data are interpolated to a 10km*10km grid,

from which the climate estimates for the vole trapping locations were derived. Interpolation works well with temperature data, which tends to show large-scale spatial correlation. Precipitation, however, may vary locally, and spatial interpolation tends to underestimate the precipitation levels, especially when precipitation is high (Vajda and Venäläinen 2003).

3.6.3 Reliability of the predictions

The accuracy of the predicted future vole population dynamics depends on the accuracy of the model and on the accuracy of the climate predictions. Fairly small differences in climate can cause large differences in vole population dynamics, and the future climate cannot be predicted with 100% accuracy. For the future predictions, the median, minimum and maximum predicted climate change, based on several climate models, and several greenhouse gas emission scenarios, were used. Therefore, it is overall likely that climate will be within the range of the scenarios considered here. However, winter climate is more difficult to predict than summer climate, and precipitation is more difficult to predict than temperature, both due to the high natural variation (Jylhä *et al.* 2009). Furthermore, the variability in temperature is predicted to decline (Jylhä *et al.* 2009), which was not considered in the models, because quantitative information on the expected variability was not available. Minimum temperatures are predicted to increase more than maximum temperatures, and the seasonal and inter-annual variability in weather is expected to decrease. Stochastic variability tends to increase the amplitude of the population fluctuations (Royama 1992), so it is possible that the decline in variability adds to the dampening of the cycle.

The performance of the model was tested 1) by dividing the data set into two halves, using one half to parameterize the model, and the other to assess the accuracy of the model predictions (III), 2) by simulating predator and vole population dynamics based on observed climate and comparing the observed and simulated dynamics (IV), and 3) the model, which was based on Finnish vole, predator, and climate data, was used to predict vole population dynamics in Sweden based on climate information (IV). The model performed well in all validation approaches. Notably, Turchin and Ellner (2000) assessed the performance of their mechanistic model in explaining the density variations in different vole populations and found that the model only worked in the northernmost populations. Nevertheless, Hanski *et al.* (2001) called the performance of the model a remarkable result. The performance of my phenomenological models did not pale in this comparison, as they reached higher R^2 value simultaneously for 32 for vole populations, although admittedly considerably less parsimoniously (III).

To summarize, the reliability of the predictions depend first and foremost on the accuracy of the data, which is undoubtedly questionable. Particularly the estimated vole-small mustelid interactions should be taken with a pinch of salt, as the small mustelid index is likely to contain an unknown amount of error. The accuracy of the model structure should be fairly good as many different

types of models were compared and thoroughly tested. The validity of the model in a different climate was shown to be acceptable: the model created realistic vole population dynamics also with climate data not used to train the model. However, the model can only predict changes within the range of observed values and therefore should not be used to predict predator-vole interactions in different biomes. Finally, the predictions can only be as reliable as the climate scenarios, which themselves contain several sources of error. The predictions given here are at best an educated guess of what might lie ahead for vole populations in northern Europe; however, they are at the moment the guess backed with the most comprehensive data published to date.

3.7   Conclusions

Climate had a profound and intricate influence on the interactions between predators and voles, and most importantly, could explain the observed geographic and temporal variation in predator-vole interactions, and in vole population dynamics. However, the proximate mechanisms through which climate influences vole population dynamics are still unclear. Some, but not all, of the climate-associated alterations in vole population dynamics could be attributed to altered predator-vole interactions, indicating that other types of ecological interactions are likely to play a role. Overall the results support the specialist predator paradigm, but suggest that the climate-dependence of the predator-vole interaction is more complex and flexible than previously considered. Most importantly, the interaction between voles and the small mustelids was not restricted to cold winters but may occur during summers, as well. The ecological impact of climate change depends on local climatic conditions: the effect of increasing temperatures in the north is different from that in the south, where the initial climate is different, the structure of the ecosystem is different, and the biota are adapted differently. Under the expected climatic conditions in 2011–2039, the model predicted Finnish and Swedish vole populations to be mostly non-cyclic. The northern populations were predicted to become dominated by seasonal dynamics, and the southern ones by increasingly variable dynamics, shifting between regular cycles, stable dynamics, and high-amplitude irruptions. According to these results, the highly regular and predictable vole cycle will eventually disappear, although in many regions, cyclicity is likely to persist and even strengthen in the near future.

Acknowledgements

44

YHTEENVETO (RÉSUMÉ IN FINNISH)

Ilmastonmuutoksen vaikutukset biologisiin vuorovaikutuksiin pohjoisen havumetsävyöhykkeen eliöyhteisöissä

Maapallon ilmakehän keskilämpötila on noussut 1900-luvun alusta lähtien ja viimeiset 30 vuotta ovat olleet todennäköisesti lämpimimmät 1400 vuoteen. Ilmastonmuutoksen ekologiset vaikutukset ovat jo havaittavissa, sillä monien lajien levinneisyysalueet tai vuodenaikaiskierrot ovat muuttuneet. Samanaikaisesti monien eliölajien väliset vuorovaikutukset ovat muuttuneet.

Sääolot voivat vaikuttaa eläinpopulaatioihin suoraan tai epäsuorasti, muuttamalla eliöyhteisön lajikoostumusta ja populaatioiden välisiä vuorovaikutuksia. Bioottisessa ympäristössä tapahtuvat muutokset vaikuttavat todennäköisesti suoria sääolojen vaikutuksia voimakkaammin eläinpopulaatioiden kannanvaihteluihin ja eliöyhteisöjen toimintaan. Erityisesti sykliset kannanvaihtelut riippuvat lajienvälisistä vuorovaikutuksista, joihin ilmastonmuutoksen oletetaan vaikuttavan. Ilmaston ja sen muutoksen mahdolliset vaikutukset eläinpopulaatioiden kannanvaihteluihin on tärkeä ymmärtää, sillä pohjoisilla alueilla monet syklisesti vaihtelevat eläinlajit aiheuttavat säännöllisesti tuhoja maa- ja metsätaloudessa sekä kantavat ihmisiinkin tarttuvia taudinaiheuttajia.

Viime aikoina säännöllisten populaatiosyklien on raportoitu hävinneen sekä Suomessa että muualla Euroopassa. Ilmiön on havaittu koskevan myyriä, sopuleita ja metsäkanalintuja, jotka ovat monien petoeläinten tärkein ravinnonlähde ja keskeinen kasviyhteisöjen koostumukseen vaikuttava kasvinsyöjäryhmä. Myyrät ovat Suomen yleisimpiä nisäkkäitä ja lukumääränsä sekä säännöllisten kannanvaihteluidensa vuoksi avainasemassa pohjoisen havumetsävyöhykkeen eliöyhteisöissä. Myyrien kannanvaihteluiden muutoksilla voi näin ollen olla voimakkaita ekologisia vaikutuksia. Myyrien ja petoeläinten välistä vuorovaikutusta pidetään keskeisenä tekijänä pohjoisen myyräsyklin synnyssä ja sen uskotaan olevan riippuvainen ilmastosta. Lumikko ja kärppä ovat ainoat pedot, jotka voivat saalistaa myyriä lumen alla, ja pitkien talvien ajatellaan voimistavan näiden eläinlajien välisiä vuorovaikutuksia ja siten niiden syklisiä kannanvaihteluita. Syklien häviämisen syyksi on ehdotettu talvien lämpenemistä: lumipeite vähenee ja lumen toistuva sulaminen ja jäätyminen muodostaa jääkerroksen maan pinnalle, mikä estää myyriä löytämästä ruokaa, vaikeuttaa lämpimänä pysymistä, ja altistaa myyrät monille pedoille. Myyräsyklejä esiintyy kuitenkin myös alueilla, joilla talvet ovat lyhyempiä ja vähälumisempia kuin Suomessa, joten talven olosuhteiden vaikutus myyrien populaatiodynamiikkaan ja myyrien ja petojen välisiin vuorovaikutuksiin on vielä hyvin epäselvä.

Tutkin ilmaston vaikutuksia myyriin sekä myyrien ja petojen välisiin vuorovaikutuksiin analysoimalla laajoja, koko Suomen kattavia eläinpopulaatio- ja ilmastoaineistoja vuosilta 1970-2011. Aineistojen perusteella kartoitin myyrien kannanvaihteluiden ja myyrien ja eri tyyppisten petojen vuorovaikutusten ajallisen ja maantieteellisen vaihtelun. Selvitin myös myyrä- ja petopopulaatioiden

sekä niiden välisten vuorovaikutusten riippuvuuden ilmastosta ja rakensin mallin, joka ennustaa myyrien ja petojen kannanvaihteluita ilmaston perusteella.

Toisin kuin on uskottu, Suomen myyräsyklit eivät ole kokonaan hävinneet, vaan paikoittain jopa voimistuneet. Pohjoisen voimakas sykli vaimeni murto-osaa entisestään 1980-luvulla, mutta näyttää nyt palanneen. Etelä- ja Länsi-Suomessa taas myyräsykli on voimistunut 1980-luvulta lähtien. Vain Itä-Suomen myyräpopulaatiot ovat siirtyneet kokonaan epäsäännöllisiin kannanvaihteluihin. Talven sääolosuhteet vaikuttivat myyrien kannanvaihteluihin yllättäen vähemmän kuin kesän sääolosuhteet. Myyrien ja petojen väliset vuorovaikutukset osoittautuivat lisäksi odotettua monimutkaisemmiksi. Kärpällä ja erityisesti lumikolla oli keskeinen rooli myyräsyklin synnyssä. Myyrien kannanvaihteluiden ajalliset ja maantieteelliset muutokset selittyivät suurelta osin myyrien ja näiden pikkupetojen välisten vuorovaikutusten muutoksilla, jotka puolestaan riippuivat ilmastosta. Pikkupedot vaikuttivat myyräpopulaatioihin odotetusti talvisin kylmässä ilmastossa, mutta kesäisin sateisessa ilmastossa. Näin ollen syklisyyttä aiheuttava myyrien ja niihin erikoistuneiden petojen välinen vuorovaikutus ei rajoittunut kylmiin ilmastoihin eikä ollut riippuvainen vain talven olosuhteista.

Malli ennusti myyräsyklin häviävän seuraavien muutaman vuosikymmenen aikana Pohjois-Euroopassa. Voimakkaiden myyrähuippujen ennustetaan vähitellen harvenevan ja lopulta häviävän Pohjois-Suomessa ja -Ruotsissa. Keski- ja Etelä-Suomessa myyrien kannanvaihteluiden ennustetaan muuttuvan epäsäännöllisiksi. Paikoittain säännöllinen ja voimakaskin sykli voi jatkua, mutta toisinaan huiput saattavat olla poikkeuksellisen suuria ja toisinaan jäädä kokonaan puuttumaan. Myyrähuippujen puuttuminen vaikuttaa todennäköisesti hyvin laajasti peto-, kasvinsyöjä- ja kasviyhteisöihin. Erityisesti pohjoisessa myyrähuiput säätelevät koko eliöyhteisön toimintaa ja niiden puuttuminen todennäköisesti johtaa myös sopulihuippujen häviämiseen, monien petolajien vähenemiseen, muihin nisäkäs- ja lintulajeihin kohdistuvan saalistuspaineen voimistumiseen ja kasvillisuuden muutoksiin. Tämän lisäksi huippujen säännöllisyyden väheneminen vaikeuttaa myyrätuhojen ja myyräkuumeriskin ennustamista. Erityisen hälyttävää on mallin ennustama epäsäännöllisten huippujen voimistuminen, mikä tarkoittaa että myyrien aiheuttamat haitat voivat kasvaa nopeasti ja niitä on vaikea ennakoida.

REFERENCES

Aars J. & Ims R.A. 2002. Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. *Ecology* 83: 3449-3456.

Ahas R., Aasa A., Menzel A., Fedotova V. & Scheifinger H. 2002. Changes in European spring phenology. *Int J Climatol* 22: 1727-1738.

Andersson M. & Erlinge S. 1977. Influence of Predation on Rodent Populations. *Oikos* 29: 591-597.

Andreassen H.P., Glorvigen P., Rémy A. & Ims R.A. 2013. New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles. *Oikos* 122: 507-515.

Angelstam P., Lindström E. & Widén P. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62: 199-208.

Angelstam P., Lindström E. & Widén P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia: occurrence and distribution. *Ecography* 8: 285-298.

Ayres M.P. & Lombardero M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ* 262: 263-286.

Beckerman A., Benton T., Ranta E., Kaitala V. & Lundberg P. 2002. Population dynamic consequences of delayed life-history effects. *Trends in Ecology & Evolution* 17: 263-269.

Berryman A. 2002. Population cycles: The case for trophic interactions. Oxford University Press, New York.

Bierman S.M., Fairbairn J.P., Petty S.J., Elston D.A., Tidhar D. & Lambin X. 2006. Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (Microtus agrestis L.). *Am Nat* 167: 583-590.

Bobretsov A.V. 2009. Dynamics of the Red Vole (Clethrionomys Rutilus, Rodentia) Number for Fifty Years in the Northern Cis-Ural Region. *Zool Zhurnal* 88: 1115-1126.

Both C., Bouwhuis S., Lessells C. & Visser M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81-83.

Both C., Van Turnhout C.A., Bijlsma R.G., Siepel H., Van Strien A.J. & Foppen R.P. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc Biol Sci* 277: 1259-1266.

Brommer J.E., Pietiäinen H. & Kolunen H. 2002. Reproduction and survival in a variable environment: Ural owls (Strix uralensis) and the three-year vole cycle. *Auk* 119: 544-550.

Brommer J.E., Pietiainen H., Ahola K., Karell P., Karstinen T. & Kolunen H. 2010. The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. *Global Change Biol* 16: 577-586.

Brook B.W. & Bradshaw C.J. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87: 1445-1451.

Bujalska G. 1985. Regulation of Female Maturation in Clethrionomys Species, with Special Reference to an Island Population of Clethrionomys-Glareolus. *Ann Zool Fenn* 22: 331-342.

Burthe S., Telfer S., Lambin X., Bennett M., Carslake D., Smith A. & Begon M. 2006. Cowpox virus infection in natural field vole Microtus agrestis populations: delayed density dependence and individual risk. *J Anim Ecol* 75: 1416-1425.

Cavanagh R.D., Lambin X., Ergon T., Bennett M., Graham I.M., van Soolingen D. & Begon M. 2004. Disease dynamics in cyclic populations of field voles (Microtus agrestis): cowpox virus and vole tuberculosis (Mycobacterium microti). *Proceedings of the Royal Society B-Biological Sciences* 271.

Cazelles B., Chavez M., Berteaux D., Ménard F., Vik J.O., Jenouvrier S. & Stenseth N.C. 2008. Wavelet analysis of ecological time series. *Oecologia* 156: 287-304.

Chase J.M. & Leibold M.A. 2002. Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416: 427-430.

Cheveau M., Drapeau P., Imbeau L. & Bergeron Y. 2004. Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. *Oikos* 107: 190-198.

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., Jedrzejewska B., Millon A., Petty S.J., Pietiainen H., Tkadlec E., Zub K. & Lambin X. 2013. Europe-Wide Dampening of Population Cycles in Keystone Herbivores. *Science* 340: 63-66.

Dahlgren J., Oksanen L., Sjodin M. & Olofsson J. 2007. Interactions between gray-sided voles (Clethrionomys rufucanus) and bilberry (Vaccinium myrtillus), their main winter food plant 2009. *Oecologia* 152: 525-532.

Dell'Arte G.L., Laaksonen T., Norrdahl K. & Korpimäki E. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecol -Int J Ecol* 31: 276-281.

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 Ecol* 25: 551-560.

Edwards M. & Richardson A.J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430: 881-884.

Elmhagen B., Ludwig G., Rushton S., Helle P. & Lindén H. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *J Anim Ecol* 79: 785-794.

Epskamp S., Cramer A.O., Waldorp L.J., Schmittmann V.D. & Borsboom D. 2012. Qgraph: Network visualizations of relationships in psychometric data. *Journal of Statistical Software* 48: 1-18.

Ergon T., Ergon R., Begon M., Telfer S. & Lambin X. 2011. Delayed density-dependent onset of spring reproduction in a fluctuating population of field voles. *Oikos* 120: 934-940.

48

Erlinge S. 1987. Predation and Noncyclicity in a Microtine Population in Southern Sweden. *Oikos* 50: 347-352.

Erlinge S., Agrell J., Nelson J. & Sandell M. 1991. Why are some Microtine Populations Cyclic while Others are Not. *Acta Theriol* 36: 63-71.

Esper J., Buentgen U., Frank D.C., Nievergelt D. & Liebhold A. 2007. 1200 Years of Regular Outbreaks in Alpine Insects. *Proc R Soc B-Biol Sci* 274: 671-679.

Fischlin A., Midgley G.F., Price J., Leemans R., Gopal B., Turley C., Rounsevell M., Dube P., Tarazona J. & Velichko A. 2007. Ecosystems, their properties, goods, and services. .

Forbes K.M., Stuart P., Mappes T., Hoset K.S., Henttonen H. & Huitu O. 2014. Diet Quality Limits Summer Growth of Field Vole Populations. *PloS one* 9: e91113.

Fox J.F. 1985. Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. *Arct Alp Res* : 199-204.

Framstad E., Stenseth N.C., Bjørnstad O.N. & Falck W. 1997. Limit cycles in Norwegian lemmings: tensions between phase–dependence and density-dependence. *Proceedings of the Royal Society of London.Series B: Biological Sciences* 264: 31-38.

Gaston K.J. 2000. Global patterns in biodiversity. *Nature* 405: 220-227.

Gilbert S., Norrdahl K., Martel J. & Klemola T. 2013. Vole damage to woody plants reflects cumulative rather than peak herbivory pressure. 50: 189-199.

Gilman S.E., Urban M.C., Tewksbury J., Gilchrist G.W. & Holt R.D. 2010. A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25: 325-331.

Hakkarainen H., Korpimäki E., Koivunen V. & Ydenberg R. 2002. Survival of male Tengmalm's owls under temporally varying food conditions. *Oecologia* 131: 83-88.

Hallett T., Coulson T., Pilkington J., Clutton-Brock T., Pemberton J. & Grenfell B. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* 430: 71-75.

Hansen T.F., Stenseth N.C., Henttonen H. & Tast J. 1999. Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. *Proc Natl Acad Sci U S A* 96: 986-991.

Hanski I. & Korpimäki E. 1995. Microtine Rodent Dynamics in Northern Europe - Parameterized Models for the Predator-Prey Interaction. *Ecology* 76: 840-850.

Hanski I. & Henttonen H. 1996. Predation on competing rodent species: a simple explanation of complex patterns. *J Anim Ecol* 65: 220-232.

Hanski I. & Henttonen H. 2002. Population cycles of small rodents in Fennoscandia. In: Berryman A. (ed.), *Population cycles: the case for trophic interactions*, Oxford University Press, New York, USA, pp. 44-68.

Hanski I., Hansson L. & Henttonen H. 1991. Specialist Predators, Generalist Predators, and the Microtine Rodent Cycle. *J Anim Ecol* 60: 353-367.

Hanski I., Henttonen H. & Hansson L. 1994. Temporal variability of population density in microtine rodents: a reply to Xia and Boonstra. *American Naturalist* 144:329-342.

Hanski I., Henttonen H., Korpimäki E., Oksanen L. & Turchin P. 2001. Small-rodent dynamics and predation. *Ecology* 82: 1505-1520.

Hansson L. 1987. An interpretation of rodent dynamics as due to trophic interactions. *Oikos* : 308-318.

Hansson L. 1999. Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. *Oikos* 86: 159-169.

Hansson L. & Henttonen H. 1985. Gradients in Density Variations of Small Rodents - the Importance of Latitude and Snow Cover. *Oecologia* 67: 394-402.

Hansson L. & Henttonen H. 1988. Rodent dynamics as community processes. *Trends in Ecology & Evolution* 3: 195-200.

Helldin J. 1999. Diet, body condition, and reproduction of Eurasian pine martens Martes martes during cycles in microtine density. *Ecography* 22: 324-336.

Helle H., Koskela E. & Mappes T. 2012. Life in varying environments: experimental evidence for delayed effects of juvenile environment on adult life history. *J Anim Ecol* 81: 573-582.

Henden J., Ims R.A. & Yoccoz N.G. 2009. Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *J Anim Ecol* 78: 636-645.

Henttonen H., Kaikusalo A., Tast J. & Viitala J. 1977. Interspecific competition between small rodents in subarctic and boreal ecosystems. *Oikos* : 581-590.

Henttonen H., Oksanen T., Jortikka A. & Haukisalmi V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos*: 353-365.

Höglind M., Thorsen S.M. & Semenov M.A. 2013. Assessing uncertainties in impact of climate change on grass production in Northern Europe using ensembles of global climate models. *Agric For Meteorol* 170: 103-113.

Hörnfeldt B. 1978. Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia* 32: 141-152.

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: analysis 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-Biological Sciences* 272: 2045-2049.

Hörnfeldt B., Carlsson B., Löfgren O. & Eklund U. 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl (Aegolius funereus). *Can J Zool* 68: 522-530.

Hörnfeldt B., Christensen P., Sandström P. & Ecke F. 2006. Long-term decline and local extinction of Clethrionomys rufocanus in boreal Sweden. *Landscape Ecol* 21: 1135-1150.

50

Howe H.F., Zorn-Arnold B., Sullivan A. & Brown J.S. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. *Ecology* 87: 3007-3013.

Huitu O., Norrdahl K. & Korpimäki E. 2004. Competition, predation and interspecific synchrony in cyclic small mammal communities. *Ecography* 27: 197-206.

Huitu O., Rousi M. & Henttonen H. 2013. Integration of vole management in boreal silvicultural practices. *Pest Manag Sci* 69: 355-361.

Huitu O., Kiljunen N., Korpimäki E., Koskela E., Mappes T., Pietiäinen H., Pöysä H. & Henttonen H. 2009. Density-dependent vole damage in silviculture and associated economic losses at a nationwide scale. *For Ecol Manage* 258: 1219-1224.

Ims R.A. & Andreassen H.P. 2000. Spatial synchronization of vole population dynamics by predatory birds. *Nature* 408: 194-196.

Ims R.A. & Fuglei E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* 55: 311-322.

Ims R.A., Henden J. & Killengreen S.T. 2008. Collapsing population cycles. *Trends in Ecology & Evolution* 23: 79-86.

Ims R.A., Yoccoz N.G. & Killengreen S.T. 2011. Determinants of lemming outbreaks. *Proc Natl Acad Sci U S A* 108: 1970-1974.

Inchausti P. & Ginzburg L.R. 2009. Maternal effects mechanism of population cycling: a formidable competitor to the traditional predator-prey view. *Philos Trans R Soc Lond B Biol Sci* 364: 1117-1124.

Jedrzejewski W., Jedrzejewska B. & Szymura L. 1995. Weasel Population Response, Home-Range, and Predation on Rodents in a Deciduous Forest in Poland. *Ecology* 76: 179-195.

Jylhä K., Fronzek S., Tuomenvirta H., Carter T.R. & Ruosteenoja K. 2008. Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. *Clim Change* 86: 441-462.

Jylhä K., Ruosteenoja K., Räisänen J., Venäläinen A., Tuomenvirta H., Ruokolainen L., Saku S. & Seitola S. 2009. Arvioita Suomen muuttuvasta ilmastosta

sopeutumistutkimuksia varten. *Ilmatieteen laitos, Raportteja* 4.

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: 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.

Karell P., Ahola K., Karstinen T., Zolei A. & Brommer J.E. 2009. Population dynamics in a cyclic environment: consequences of cyclic food abundance on tawny owl reproduction and survival. *J Anim Ecol* 78: 1050-1062.

Kauhala K. & Helle P. 2007. Metsäjäniskanta pienentynyt voimakkaasti. *Riista- ja kalatalous. Selvityksiä* 3: 1-12.

Kausrud K.L., Mysterud A., Steen H., Vik J.O., Ostbye E., Cazelles B., Framstad E., Eikeset A.M., Mysterud I., Solhoy T. & Stenseth N.C. 2008. Linking climate change to lemming cycles. *Nature* 456: 93-U3.

Kellomäki S., Karjalainen T. & Väisänen H. 1997. More timber from boreal forests under changing climate? *For Ecol Manage* 94: 195-208.

Kellomäki S., Maajärvi M., Strandman H., Kilpeläinen A. & Peltola H. 2010. Model computations on the climate change effects on snow cover, soil moisture and soil frost in the boreal conditions over Finland. *Silva Fenn* 44: 213-233.

Kendall,B.E., Briggs,C.J., Murdoch,W.W., Turchin,P., Ellner,S.P., McCauley,E., Nisbet,R.M. & Wood,S.N. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* 80: 1789-1805.

Kent A., Plesner Jensen S. & Doncaster C.P. 2005. Model of microtine cycles caused by lethal toxins in non-preferred food plants. *J Theor Biol* 234: 593-604.

Klemola T., Koivula M., Korpimäki E. & Norrdahl K. 2000. Experimental tests of predation and food hypotheses for population cycles of voles. *Proceedings of the Royal Society B-Biological Sciences* 267: 351-356.

Klemola T., Tanhuanpaa M., Korpimäki E. & Ruohomaki K. 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. *Oikos* 99: 83-94.

Koca D., Smith B. & Sykes M.T. 2006. Modelling regional climate change effects on potential natural ecosystems in Sweden. *Clim Change* 78: 381-406.

Korpela K., Sundell J. & Ylönen H. 2010. Density dependence of infanticide and recognition of pup sex in male bank voles. *Behaviour* 147: 871-881.

Korpimäki E. & Norrdahl K. 1989a. Avian predation on mustelids in Europe 1: occurrence and effects on body size variation and life traits. *Oikos* : 205-215.

Korpimäki E. & Norrdahl K. 1989b. Avian Predation on Mustelids in Europe 2: Impact on Small Mustelid and Microtine Dynamics: A Hypothesis. *Oikos* : 273-276.

Korpimäki E. & Norrdahl K. 1991a. Do Breeding Nomadic Avian Predators Dampen Population Fluctuations of Small Mammals. *Oikos* 62: 195-208.

Korpimäki E. & Norrdahl K. 1991b. Numerical and Functional-Responses of Kestrels, Short-Eared Owls, and Long-Eared Owls to Vole Densities. *Ecology* 72: 814-826.

Korpimäki E., Norrdahl K. & Rintajaskari T. 1991. Responses of Stoats and Least Weasels to Fluctuating Food Abundances - is the Low Phase of the Vole Cycle due to Mustelid Predation. *Oecologia* 88: 552-561.

Korpimäki E., Norrdahl K., Huitu O. & Klemola T. 2005. Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proc Biol Sci* 272: 193-202.

Korpimäki 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-Biological Sciences* 269: 991-997.

52

Korpimäki E., Oksanen L., Oksanen T., Klemola T., Norrdahl K. & Banks P.B. 2005. Vole cycles and predation in temperate and boreal zones of Europe. *J Anim Ecol* 74: 1150-1159.

Korslund L. & Steen H. 2006. Small rodent winter survival: snow conditions limit access to food resources. *J Anim Ecol* 75: 156-166.

Krebs C.J. 2013. *Population fluctuations in rodents.* University of Chicago Press.

Laine K.M. & Henttonen H. 1987. Phenolics/nitrogen ratios in the blueberry Vaccinium myrtillus in relation to temperature and microtine density in Finnish Lapland. *Oikos* : 389-395.

Lambin X., Petty S.J. & MacKinnon J.L. 2000. Cyclic dynamics in field vole populations and generalist predation. *J Anim Ecol* 69: 106-118.

Lambin X., Bretagnolle V. & Yoccoz N.G. 2006. Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern? *J Anim Ecol* 75: 340-349.

Lehikoinen A., Byholm P., Ranta E., Saurola P., Valkama J., Korpimäki E., Pietiäinen H. & Henttonen H. 2009. Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos* 118: 829-836.

Lehikoinen A., Ranta E., Pietiainen H., Byholm P., Saurola P., Valkama J., Huitu O., Henttonen H. & Korpimäki E. 2011. The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. *Oecologia* 165: 349-355.

Lewin-Koh N.J., Bivand R., Pebesma E., Archer E., Baddeley A., Bibiko H., Dray S., Forrest D., Friendly M. & Giraudoux P. 2011. maptools: Tools for reading and handling spatial objects. *R package version 0.8-10, URL http://CRAN.R-project.org/package= maptools* .

Linden H., Helle E., Helle P. & Wikman M. 1996. Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Research* 49: 4-11.

Lindström E. 1983. Condition and growth and Red Foxes (Vulpes vulpes) in relation to food supply. *J Zool* 199: 117-122.

Lindström E. 1988. Reproductive effort in the red fox, Vulpes vulpes, and future supply of a fluctuating prey. *Oikos* : 115-119.

Ludwig G. 2007. Mechanisms of population declines in boreal forest grouse. *Jyväskylä studies in biological and environmental science* 176: 1456-9701.

Ludwig G.X., Alatalo R.V., Helle P., Lindén H., Lindström J. & Siitari H. 2006. Short-and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proceedings of the Royal Society B: Biological Sciences* 273: 2009-2016.

Massey F.P., Smith M.J., Lambin X. & Hartley S.E. 2008. Are silica defences in grasses driving vole population cycles? *Biol Lett* 4: 419-422.

Menzel A., Sparks T.H., Estrella N., Koch E., Aasa A., Ahas R., ALM-KÜBLER K., Bissolli P., Braslavská O. & Briede A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biol* 12: 1969-1976.

Millon A., Petty S.J., Little B., Gimenez O., Cornulier T. & Lambin X. 2014. Dampening prey cycle overrides the impact of climate change on predator population dynamics: a long-term demographic study on tawny owls. *Global Change Biol.*

Moran P. 1953. The statistical analysis of the Canadian Lynx cycle. *Aust J Zool* 1: 291-298.

Nemani R.R., Keeling C.D., Hashimoto H., Jolly W.M., Piper S.C., Tucker C.J., Myneni R.B. & Running S.W. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300: 1560-1563.

Niklasson B., Nyholm E., Feinstein R.E., Samsioe A. & Hörnfeldt B. 2006. Diabetes and myocarditis in voles and lemmings at cyclic peak densities - induced by Ljungan virus? *Oecologia* 150: 1-7.

Norrdahl K. & Korpimäki E. 1995. Mortality factors in a cyclic vole population. *Proceedings of the Royal Society of London.Series B: Biological Sciences* 261: 49-53.

Norrdahl K. & Korpimäki E. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology* 79: 226-232.

Norrdahl K. & Korpimäki E. 2002. Seasonal changes in the numerical responses of predators to cyclic vole populations. *Ecography* 25: 428-438.

Oksanen L. & Oksanen T. 1992. Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. *Ecography* 15: 226-236.

Oksanen T., Oksanen L., Schneider M. & Aunapuu M. 2001. Regulation, cycles and stability in northern carnivore-herbivore systems: back to first principles. *Oikos* 94: 101-117.

Olofsson J., Tømmervik H. & Callaghan T.V. 2012. Vole and lemming activity observed from space. *Nature Climate Change* 2: 880-883.

Ottersen G., Planque B., Belgrano A., Post E., Reid P.C. & Stenseth N.C. 2001. Ecological effects of the North Atlantic oscillation. *Oecologia* 128: 1-14.

Parmesan C. & Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Parmesan C., Ryrholm N., Stefanescu C., Hill J.K., Thomas C.D., Descimon H., Huntley B., Kaila L., Kullberg J. & Tammaru T. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Pebesma E.J. 2004. Multivariable geostatistics in S: the gstat package. *Computers & Geosciences* : 683-691.

Pinheiro J., Bates D., DebRoy S., Sarkar D. & the R Development Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-108.

Post E. & Forchhammer M.C. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philos Trans R Soc Lond B Biol Sci* 363: 2369-2375.

Pulliainen E. & Ollinmaki P. 1996. A long-term study of the winter food niche of the pine marten Martes martes in northern boreal Finland. *Acta Theriol* 41: 337-352.

Questad E.J. & Foster B.L. 2007. Vole disturbances and plant diversity in a grassland metacommunity. *Oecologia* 153: 341-351.

R Core Team. 2012. R: A language and environment for statistical computing. .

Reif V., Tornberg R., Jungell S. & Korpimäki E. 2001. Diet variation of common buzzards in Finland supports the alternative prey hypothesis. *Ecography* 24: 267-274.

Reynolds J.J.H., Lambin X., Massey F.P., Reidinger S., Sherratt J.A., Smith M.J., White A. & Hartley S.E. 2012. Delayed induced silica defences in grasses and their potential for destabilising herbivore population dynamics. *Oecologia* 170: 445-456.

Rossow H., Sissonen S., Koskela K., Kinnunen P., Hemmilä H., Niemimaa J., Huitu O., Kuusi M., Vapalahti O., Henttonen H. & Nikkari S. 2014. Detection of Francisella tularensis in voles in Finland. *Vector-Borne and Zoonotic Diseases* 14: 193-198.

Royama T. 1992. *Analytical Population Dynamics.* Chapman & Hall, London.

Rydgren K., Okland R.H., Pico F.X. & de Kroon H. 2007. Moss species benefits from breakdown of cyclic rodent dynamics in boreal forests. *Ecology* 88: 2320-2329.

Saitoh T., Stenseth N.C. & Björnstad O.N. 1998. The population dynamics of the vole Clethrionomys rufocanus in Hokkaido, Japan. *Res Popul Ecol* 40: 61-76.

Salamolard M., Butet A., Leroux A. & Bretagnolle V. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* 81: 2428-2441.

Saurola P. 2008. Monitoring birds of prey in Finland: A summary of methods, trends, and statistical power. *Ambio* 37: 413-419.

Schweiger O., Settele J., Kudrna O., Klotz S. & Kühn I. 2008. Climate change can cause spatial mismatch of trophically interacting species. *Ecology* 89: 3472-3479.

Selås V., Kobro S. & Sonerud G.A. 2013. Population fluctuations of moths and small rodents in relation to plant reproduction indices in southern Norway. *Ecosphere* 4: art123.

Serreze M., Walsh J., Chapin Iii F., Osterkamp T., Dyurgerov M., Romanovsky V., Oechel W., Morison J., Zhang T. & Barry R. 2000. Observational evidence of recent change in the northern high-latitude environment. *Clim Change* 46: 159-207.

Shorrocks B., Albon S., Tkadlec E. & Zejda J. 1998. Density-dependent life histories in female bank voles from fluctuating populations. *J Anim Ecol* 67: 863-873.

Smith M.J., White A., Lambin X., Sherratt J.A. & Begon M. 2006. Delayed density-dependent season length alone can lead to rodent population cycles. *Am Nat* 167: 695-704.

Smith M.J., White A., Sherratt J.A., Telfer S., Begon M. & Lambin X. 2008. Disease effects on reproduction can cause population cycles in seasonal environments. *J Anim Ecol* 77: 378-389.

Soja A.J., Tchebakova N.M., French N.H., Flannigan M.D., Shugart H.H., Stocks B.J., Sukhinin A.I., Parfenova E., Chapin III F.S. & Stackhouse Jr P.W. 2007. Climate-induced boreal forest change: predictions versus current observations. *Global Planet Change* 56: 274-296.

Solonen T. 2005. Breeding of the Tawny Owl Strix aluco in Finland: responses of a southern colonist to the highly variable environment of the North. *Ornis Fenn* 82: 97-106.

Soveri T., Henttonen H., Rudback E., Schildt R., Tanskanen R., Husu-Kallio J., Haukisalmi V., Sukura A. & Laakkonen J. 2000. Disease patterns in field and bank vole populations during a cyclic decline in central Finland. *Comp Immunol Microbiol Infect Dis* 23: 73-89.

Stenseth N.C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87: 427-461.

Stenseth N., Björnstad O. & Saitoh T. 1996. A gradient from stable to cyclic populations of Clethrionomys rufocanus in Hokkaido, Japan. *Proceedings of the Royal Society of London Series B-Biological Sciences* 263: 1117-1126.

Stenseth N., Björnstad O. & Saitoh T. 1998. Seasonal forcing on the dynamics of Clethrionomys rufocanus: Modeling geographic gradients in population dynamics. *Researches on Population Ecology* 40: 85-95.

Stenseth N.C., Mysterud A., Ottersen G., Hurrell J.W., Chan K.S. & Lima M. 2002. Ecological effects of climate fluctuations. *Science* 297: 1292-1296.

Stenseth N.C., Chan K.S., Tong H., Boonstra R., Boutin S., Krebs C.J., Post E., O'Donoghue M., Yoccoz N.G., Forchhammer M.C. & Hurrell J.W. 1999. Common dynamic structure of canada lynx populations within three climatic regions. *Science* 285: 1071-1073.

Stocker T., Qin D., Plattner M., Tignor M., Allen S., Boschung J., Nauels A., Xia Y., Bex V. and Midgley P. 2013. Climate change 2013: The physical science basis. *Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Summary for Policymakers*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

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.

Summerhayes V. 1941. The effect of voles (Microtus agrestis) on vegetation. *The Journal of Ecology* : 14-48.

Sundell J., Huitu O., Henttonen H., Kaikusalo A., Korpimäki E., Pietiainen H., Saurola P. & Hanski I. 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *J Anim Ecol* 73: 167-178.

56

Sundell J., O'Hara R.B., Helle P., Hellstedt P., Henttonen H. & Pietiainen H. 2013. Numerical response of small mustelids to vole abundance: delayed or not? *Oikos* 122: 1112-1120.

Tanner J.T. 1966. Effects of population density on growth rates of animal populations. *Ecology* : 733-745.

Taylor R.A., White A. & Sherratt J.A. 2013. How do variations in seasonality affect population cycles? *Proc Biol Sci* 280: 20122714.

Thakur M.P., Reich P.B., Fisichelli N.A., Stefanski A., Cesarz S., Dobies T., Rich R.L., Hobbie S.E. & Eisenhauer N. 2014. Nematode community shifts in response to experimental warming and canopy conditions are associated with plant community changes in the temperate-boreal forest ecotone. *Oecologia* 175: 713-723.

Thuiller W., Lavorel S., Sykes M.T. & Araújo M.B. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Divers Distrib* 12: 49-60.

Telfer S., Bennett M., Bown K., Carslake D., Cavanagh R., Hazel S., Jones T. & Begon M. 2005. Infection with cowpox virus decreases female maturation rates in wild populations of woodland rodents. *Oikos* 109: 317-322.

Tietäväinen H., Tuomenvirta H. & Venäläinen A. 2010. Annual and seasonal mean temperatures in Finland during the last 160 years based on gridded temperature data. *Int J Climatol* 30: 2247-2256.

Tkadlec E. & Stenseth N.C. 2001. A new geographical gradient in vole population dynamics. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 1547-1552.

Tuomenvirta H. 2004. Reliable estimation of climatic variations in Finland. *Finnish Meteorological Institute Contributions* 43: 1-158.

Turchin P. & Hanski I. 1997. An empirically based model for latitudinal gradient in vole population dynamics. *Am Nat* 149: 842-874.

Turchin P. & Ellner S.P. 2000. Living on the edge of chaos: Population dynamics of Fennoscandian voles. *Ecology* 81: 3099-3116.

Turchin P. & Hanski I. 2001. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol Lett* 4: 267-276.

Turchin P., Oksanen, L., Ekerholm, P., Oksanen, T. & Henttonen, H. 2000. Are lemmings prey or predators? *Nature* 405: 562-565.

Vajda A. & Venäläinen A. 2003. The influence of natural conditions on the spatial variation of climate in Lapland, northern Finland. *Int J Climatol* 23: 1011-1022.

Walther G., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J., Fromentin J., Hoegh-Guldberg O. & Bairlein F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.

Van der Putten W.H., Macel M. & Visser M.E. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philos Trans R Soc Lond B Biol Sci* 365: 2025-2034.

Førland E., Allerup P., Dahlström B., Elomaa E., Jonsson T., Madsen H., Perälä J., Rissanen R., Vedin H. & Vejen F. Manual For Operational Correction Of Nordic Precipitation Data. Norwegian Meterological Institute Oslo.

Venables W. & Ripley B. 2002. *Modern Applied Statistics with S.* Springer, New York.

Venäläinen A., Tuomenvirta H. & Drebs A. 2005. Finnish climate data set 1961-2000 description and illustrations. *Finnish Meteorological Institute Reports* 5.

Virkkala R. & Lehikoinen A. 2014. Patterns of climate-induced density shifts of species: poleward shifts faster in northern boreal birds than in southern birds. *Global Change Biol* .

Volney W.J.A. & Fleming R.A. 2000. Climate change and impacts of boreal forest insects. *Agric , Ecosyst Environ* 82: 283-294.

Zhao M. & Running S.W. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329: 940-943.

Zub K., Jedrzejewska B., Jedrzejewski W. & Barton K. 2012. Cyclic voles and shrews and non-cyclic mice in a marginal grassland within European temperate forest. *Acta Theriol* 57: 205-216.

ORIGINAL PAPERS

I

NONLINEAR EFFECTS OF CLIMATE ON BOREAL RODENT DYNAMICS: MILD WINTERS DO NOT NEGATE HIGH-AMPLITUDE CYCLES

by

Katri Korpela, Maria Delgado, Heikki Henttonen, Erkki Korpimäki, Esa
Koskela, Otso Ovaskainen, Hannu Pietiäinen, Janne Sundell, Nigel Yoccoz &
Otso Huitu 2013

II

**PREDATOR-VOLE INTERACTIONS IN NORTHERN EUROPE:
THE ROLE OF SMALL MUSTELIDS REVISED**

by

Katri Korpela, Pekka Helle, Heikki Henttonen, Erkki Korpimäki, Esa Koskela,
Otso Ovaskainen, Hannu Pietiäinen, Janne Sundell, Jari Valkama & Otso Huitu
2014

Proceedings of the Royal Society B

III

CLIMATE AS A DETERMINANT OF PREDATOR-VOLE DYNAMICS IN THE BOREAL ECOSYSTEM

by

Katri Korpela, Pekka Helle, Heikki Henttonen, Erkki Korpimäki, Esa Koskela,
Otso Ovaskainen, Hannu Pietiäinen, Janne Sundell, Jari Valkama & Otso Huitu
2014

Manuscript

IV

PREDICTING THE POPULATION DYNAMICS OF VOLES IN THE BOREAL ECOSYSTEM UNDER CLIMATE CHANGE

by

Katri Korpela, Pekka Helle, Heikki Henttonen, Erkki Korpimäki, Esa Koskela, Otso Ovaskainen, Hannu Pietiäinen, Janne Sundell, Jari Valkama & Otso Huitu
2014

Manuscript