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ABSTRACT

The size of an animal population is determined by the birth rate, mortality, and movement of individuals between populations. These demographic parameters, in turn, are affected by internal and external factors. Internal factors include, for example, the density and the sex ratio of the focal population. External factors can be divided to biotic and abiotic factors. In this thesis, I study the population dynamics of the Eurasian red squirrel (*Sciurus vulgaris*) and factors affecting it on different scales by utilizing snow-track data, old hunting data and data on nest box occupancy. The red squirrel is widely distributed and common in boreal coniferous forests, and it acts both as a seed disperser and as an alternative prey for several predator species at the low phases of the vole cycle. It has also been an important game mammal, and red squirrel hunting was popular in Finland until the mid-1900s. The results of my thesis show that red squirrel populations fluctuate synchronously within hundreds of kilometers, and that this synchrony is driven by similarly fluctuating and spatially autocorrelated spruce (*Picea abies*) cone crop. The main predators, the pine marten (*Martes martes*) and the goshawk (*Accipiter gentilis*), on the other hand, do not negatively affect red squirrel numbers on the population level. On a smaller scale, however, both the red squirrel and the flying squirrel (*Pteromys volans*) more likely occupied nest boxes that were far from the nests of avian predators. Thus, the squirrels and their predators are negatively associated on individual level, but the red squirrel and its predators are positively associated on a larger scale. The variation in red squirrel numbers between census sites and years was most strongly affected by spruce cone crop. However, cone crop did not explain the remarkable variations in the red squirrel sex ratio, which were demonstrated by the re-analysis of old hunting data. Overall, food availability emerges as the most significant determinant of red squirrel population density, exceeding the direct and indirect effects of predators. I also found out that the red squirrel is well adapted to human-altered landscape and may even favor mosaic-like areas, even though it is arboreal and adapted to a life in the forest canopy. Both the snow-track data and nest box data suggest that there are more red squirrels near human settlement and in agricultural areas than in continuous forests. A mosaic-like landscape provides red squirrels with alternative food resources, which makes them less dependent on the highly variable conifer cone crop. The apparent preference for agricultural areas by both the red squirrel and the flying squirrel may be partially explained by the higher productivity of forest edges. Even though a red squirrel is still a common sight in backyards and bird-feeding sites, it seems that the species has declined in forests. The analysis of the snow-track data from Finland and north-western Russia revealed that the red squirrel declined in most parts of the 1000000 km²-study area between 1996 and 2012. This alarming trend is partially due to the global warming. I found that the red squirrel population growth rate was lowest in those regions where winters warmed the most. Other climatic parameters, deforestation, and the simultaneous

increase in pine marten populations did not explain the decline of the red squirrel. The exact mechanism of how winter warming is detrimental for the red squirrel calls for further studies. The Finnish snow-track data from 1989 to 2017 shows that the red squirrel increased in Southern Finland but declined in other parts of the country. Drawn together, the results of this thesis show that synchrony occurs between red squirrel populations on a scale of hundreds of kilometers, and that the large-scale population dynamics are driven by conifer seed crop while predators have only a minor role. The red squirrel has adapted well to many anthropogenic changes, such as built areas and agricultural fields fragmenting forests, but the global warming seems to pose a threat to it. Studying the changes in red squirrel populations can help understand ecosystems of the boreal forests and the way anthropogenic changes affect them.

TIIVISTELMÄ

Eläinpopulaation sisäiset ja ulkoiset tekijät vaikuttavat populaatiokokoon syntyvyyden, kuolleisuuden ja muuttoliikkeen kautta. Sisäisiä eli populaatioon itseensä liittyviä tekijöitä ovat esimerkiksi sukupuolijakauma ja tiheys. Ulkoiset tekijät puolestaan voidaan jakaa eliöiden välisiin vuorovaikutuksiin ja ympäristötekijöihin. Tässä väitöskirjassa tarkastelen oravan (*Sciurus vulgaris*) populaatiodynamiikkaa ja siihen vaikuttavia tekijöitä eri mittakaavoissa lumijälkiaineistojen, vanhojen metsästysaineistojen ja pönttöjen asutusaineistojen perusteella. Orava on yleinen ja laajalle levinnyt pohjoisella havumetsävyöhykkeellä, ja sillä on tärkeä rooli ekosysteemissä puiden siementen levittäjänä ja monien petojen vaihtoehtoisena saalislajina myyräkantojen ollessa alhaalla. Se on ollut myös tärkeä riistaeläin Suomessa aina 1900-luvun puoliväliin saakka. Tutkimuksissani selvisi, että oravapopulaatioiden koko vaihtelee samanaikaisesti ja -suuntaisesti satojen kilometrien laajuisilla alueilla, ja että tämän synkronisen vaihtelun syy on samalla tavalla voimakkaasti tilassa autokorreltoitunut kuusen (*Picea abies*) käpysato. Oravan luontaisilla pääpedoilla, eli näädällä (*Martes martes*) ja kanahaukalla (*Accipiter gentilis*), ei puolestaan havaittu negatiivista vaikutusta oravamääriin populaatiotasolla. Pienemmässä mittakaavassa tarkasteltuna orava, ja myös liito-orava (*Pteromys volans*), kuitenkin käyttivät eniten sellaisia pönttöjä, jotka sijaitsivat kaukana petolintujen pesistä. Yksilötasolla oravat siis välttivät petoja, kun taas laajemmassa mittakaavassa orava ja sen saalistajat esiintyivät runsaina samoilla alueilla. Käpysato vaikutti myös voimakkaasti oravan runsauden vaihteluun eri laskenta-alueiden ja vuosien välillä. Käpysato ei kuitenkaan ollut yhteydessä oravan sukupuolijakaumaan, joka vaihteli laajoilla alueilla vanhan metsästysaineiston uudelleenanalysoinnin perusteella. Joka tapauksessa lajien välisistä vuorovaikutuksista ravinnon saatavuus ja sen vaihtelu olivat tärkeämpiä tekijöitä oravakantojen säätelyssä kuin petojen aiheuttama kuolleisuus tai petojen läsnäolon epäsuorat vaikutukset. Lisäksi, vaikka orava on sopeutunut elämään puissa ja on selkeästi metsälaji, se vaikuttaa sietävän hyvin ja jopa hyötyvän ihmisen muokkaamasta ympäristöstä. Oravia havaittiin enemmän lähellä ihmisasutusta ja maatalousympäristöä sekä lumijälki- että pönttöaineistoissa. Mosaiikkimainen, monipuolinen ympäristö tarjoaa oraville vaihtoehtoisia ravintoresursseja, jolloin ne eivät ole yhtä riippuvaisia voimakkaasti vaihtelevasta kuusen käpysadosta kuin yhtenäisillä metsäalueilla. Valoisat, peltojen rajaamat metsänreunat saattavat olla muuta metsää tuottoisampia alueita, mikä selittäisi näennäisen avoimien alueiden suosimisen sekä oravalla että liito-oravalla. Vaikka oravat ovat yleinen näky ihmisten pihapiireissä, ne vaikuttavat vähentyneen metsissä. Suomen ja Luoteis-Venäjän lumijälkiaineistoista paljastui, että oravakannat laskivat suurimmassa osassa lähes miljoonan neliökilometrin tutkimusaluetta vuosien 1996–2012 välillä. Osasyys tähän huolestuttavaan kehitykseen vaikutti olevan ilmastonmuutos. Havaittiin, että oravan populaation kasvukerroin oli pienin niillä alueilla, joissa talvet lämpenivät eniten. Muut tarkastellut ilmastomuuttujat, metsien

hakkuut ja nädän samanaikainen runsastuminen eivät olleet yhteydessä oravakannan laskuun. Ilmastonmuutoksen tarkka vaikutusmekanismi vaatii lisää tutkimuksia. Suomen lumijälkiaineiston perusteella orava runsastui Etelä-Suomessa vuosien 1989–2017 välillä, mutta kanta on ollut laskussa muissa osissa maata. Väitöskirjani tulokset osoittavat, että oravien määrä vaihtelee synkronisesti satojen kilometrien laajuisilla alueilla, ja että laajan mittakaavan populaatiodynamiikka on vahvasti riippuvainen havupuiden siemensadosta, kun taas petojen rooli on verraten vähäinen. Orava on sopeutunut moniin ihmisen aiheuttamiin muutoksiin, kuten maatalouden pirstomaan maisemaan ja asutuksen läheisyyteen, mutta ilmastonmuutos saattaa vaikuttaa oraviin haitallisesti. Oravan kannanvaihtelujen tutkiminen auttaa osaltaan ymmärtämään pohjoisten havumetsien ekosysteemien toimintaa ja ihmisen vaikutuksia niissä sekä ilmaston että maisemarakenteen muutosten kautta.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications and manuscript, which are referred to in the text by their Roman numerals:

- I** **Turkia T**, Korpimäki E, Villers A, Selonen V (2018) Predation risk landscape modifies flying and red squirrel nest site occupancy independently of habitat amount. *PLoS ONE* 13: e0194624.
- II** **Turkia T**, Selonen V, Brommer JE (2016) Large-scale spatial synchrony in red squirrel (*Sciurus vulgaris*) sex ratios. *Journal of Mammalogy* 97: 744–752.
- III** **Turkia T***, Jousimo J*, Rintala J, Tiainen J, Helle P, Hokkanen T, Valkama J, Selonen V. Large-scale spatial synchrony in red squirrel populations driven by a bottom-up effect. *Manuscript*.
- IV** **Turkia T**, Selonen V, Danilov P, Kurhinen J, Ovaskainen O, Rintala J, Brommer JE (2018) Red squirrels decline in abundance in the boreal forests of Finland and NW Russia. *Ecography* 41: 1370–1379.

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1. INTRODUCTION

1.1 Population ecology

Why and how populations change over time and space is a key interest for animal ecologists. If the birth of new individuals and the immigration from other populations are at balance with the mortality rate and emigration, the focal population remains at the same size. If, however, more individuals leave the population either through death or emigration than are recruited by birth or immigration, the population declines, and if the recruitment exceeds loss of individuals, the population increases (e.g. Begon et al. 1996). Natural populations are rarely stable over short time periods, but undergo fluctuations in size. In the longer term, the population may still remain stable (fluctuate around a stable equilibrium), or then either an increasing or a decreasing trend can emerge from the smaller scale fluctuations. The change in population size or density from one moment to the next can be quantified with population growth rate.

The population growth rate is affected by a number of internal and external factors. Internal factors, i.e. those related to the population itself, include its density (density dependent growth rate) and demographic structure. For example, a sex ratio that is biased from optimum can hinder reproduction and diminish growth. Sex ratio at the age of reproduction can be biased due to different mortality of juvenile males and females, but can also be biased at the time of birth, if mothers adaptively adjust the sex ratio of their offspring (Trivers & Willard 1973, Komdeur et al. 1997, Sheldon & West 2004). External factors relate to interactions with other species and the impact of the environment, as discussed below.

1.2 Biotic and abiotic factors affecting populations

Individual animals are dependent on food resources and are, in most cases, themselves food for other animals higher up in the food web. These interactions with other trophic levels manifest themselves as bottom-up and top-down effects at the population level. Bottom-up effects refer to how food availability controls the reproduction and survival of animals, and top-down effects refer to the control exerted by predators on the populations of their prey. The relative importance of these forces is the topic of a vast body of ecological literature (e.g. Hunter & Price 1992, Vucetich & Peterson 2004, Grippeberg & Roslin 2007, Laundré et al. 2014, Pasanen-Mortensen et al. 2017).

Interactions within the same trophic level include intra- and interspecific competition for resources such as food and shelter. All the species involved in biotic interactions are also affected by their shared environment, i.e. habitat characteristics and abiotic factors, of which the most obvious are temperature and precipitation. If a species at a lower trophic level is affected, for example, by the temperature, the effects may cascade up the trophic levels even though the species at higher levels would not be sensitive to the change in temperature *per se* themselves. This is the case with the Eurasian red squirrel (*Sciurus vulgaris*, hereafter red squirrel) and their main food resource, the seeds of the Norway

spruce (*Picea abies*, hereafter spruce), the production of which is greatly affected by summer temperature.

The word habitat is derived from the Latin word *habitare*, meaning ‘to inhabit’, and literally refers to the entity of the environment in which an organism lives. Thus, habitat quality consists of all features of the surrounding environment: abiotic factors, other organisms, and the functioning ecosystem that they form. For example, the habitat “mature boreal coniferous forest” encompasses the typical temperature and precipitation patterns in these latitudes, the animal and plant species that live there, and even their age class in the case of trees, and so on. Considering the fundamental importance of the habitat for an animal, it is not surprising that habitat *loss* is considered the most important reason for population declines worldwide (e.g. Brooks et al. 2002), along with another severe global threat to the biodiversity, which is the ongoing climate change (Thomas et al. 2004, Doney et al. 2012, Dirzo et al. 2014).

When choosing a habitat, animals face trade-offs between resource availability, predation risk, and other specific habitat characteristics. Natural selection favors optimization of these effects on fitness in different habitats (Lima 2002). The direct (lethal) and indirect (non-lethal) effects of predators may affect spatial patterns of prey individuals and, ultimately, the whole population (Zanette et al. 2011, Laundré et al. 2014). Together, habitat fragmentation and predation pressure may modify population densities more or in a different manner than either factor alone (Schneider 2001, Ryall & Fahrig 2006, Gorini et al. 2012). This highlights the importance of considering both factors when aiming to understand the distribution of animals in space (Dupke et al. 2017).

1.3 Spatial synchrony in animal populations

Spatial autocorrelation occurs when the values of a variable show a systematic pattern through space. In nature, spatial autocorrelation occurs in most environmental variables so that nearby measurements tend to be more similar than measurements from random points. Often this spatial autocorrelation is considered a nuisance that makes analysing ecological data difficult because it violates the assumption of independent observations that underlies statistical analysis techniques. However, spatial autocorrelation itself can also be interesting to study, and not only something that has to be accounted for in analyses. The strength and spatial range of autocorrelation in population dynamics can hint on an underlying mechanism driving similar trends in nearby populations. When changes in two or more populations occur simultaneously, these populations are considered to be in synchrony (Liebhold et al. 2004). This kind of spatial synchrony between conspecific animal populations, a special case of spatial autocorrelation, may be caused by dispersal (Ranta et al. 1995, Kendall et al. 2000), nomadic predators (Norrdahl & Korpimäki 1996, Korpimäki et al. 2005), trophic interactions with another species that also shows synchrony (Byholm et al. 2002, Satake et al. 2004, Cattadori et al. 2005), or spatial autocorrelation of an environmental variable that affects the

populations in question. This synchronizing effect of underlying environmental conditions, for example temperature, is called the Moran effect (Moran 1953, Royama 1992). Indeed, climate can cause synchronization of populations that are separated by distances up to 1000 kilometers (Post & Forchhammer 2002).

1.4 The aims of the thesis

The red squirrel, being a wide-spread and common mammal, makes a good study species for focusing on population ecology on a large spatiotemporal scale. In Finland, it has been an important animal both culturally and commercially, and was hunted for its fur especially in the first half of the 20th century. Because of its status as a game animal, exceptional records exist of its abundance from decades; previously based on hunting records and later on the meticulous snow-track censuses, where also red squirrel tracks are counted, even though it is not a popular game animal anymore. In this thesis, my aim was to study the (relative) effects of the top-down and bottom-up regulators as well as the environmental and abiotic factors on various aspects of the red squirrel populations making use of the vast data sets that exist. Chapters **I-IV** of this thesis describe occupancy patterns in a heterogeneous landscape, sex ratio, spatial synchrony, year-to-year fluctuation in abundance, and long-term trend, mostly on a large spatiotemporal scale.

In Chapter **I**, I studied the effects of habitat type and modelled predation risk on nest box occupancy by red squirrels and compared the results to those of flying squirrels (*Pteromys volans*) in the same study area, Kauhava, in central Finland. This is the only chapter featuring the flying squirrel; in other parts of this thesis my focus is solely on the red squirrel. Here, I was interested in the competing needs of squirrels to settle in a high-quality habitat and avoid predation, when they share a preferred forest type with their main avian predators. The mosaic-like nature of the study area also facilitates the study of how squirrels react to human-altered habitats, such as farmland, clear cuts, sapling areas, and built areas. I also wished this study to yield results that could be used in the protection of the near-threatened flying squirrel, because knowledge of habitat use and susceptibility to predation can potentially be applied to conservation measures. I was also interested in whether the red squirrels in our study area adjust their habitat use from spruce- to Scots pine -dominated (*Pinus sylvestris*, hereafter pine) forests according to the pronounced fluctuations in spruce cone crop.

The topic of Chapter **II** is the large-scale variation in the red squirrel sex ratio that has been documented by Lampio (1965), who studied the skins sold in fur stores. I re-analysed his data, and to tried to find an explanation to the deviations from 1:1 sex ratio. Following the Trivers and Willard –hypothesis (TWH; Trivers & Willard 1973), I proposed that the availability of food, which is strongly spatially autocorrelated and varies remarkably from year to year, could explain biases in the sex ratio. Shortly, the TWH is based on the fact that body condition affects reproductive success more in males than in females in a promiscuous or polygynous mating system. For example, in the case

of the red squirrel, which has a polygynous–promiscuous mating system (Lurz et al. 2005), the highest quality males account for most of the matings (Wauters et al. 1990). Assuming that the condition of the mother correlates with that of her offspring (through the level of parental investment), females who are in poor condition and can invest little in their offspring will get more grandchildren if they produce a daughter than a son. Therefore, an abundant cone crop could lead to a male-biased and a crop failure to a female-biased offspring sex ratio through variations in maternal condition.

Both Chapters **III** and **IV** are built upon analysing extensive snow-track census data (2.3.1 in Materials and methods). Here, changes in the red squirrel snow-track density are used as an index of changes in the red squirrel abundance or the population density. The exact relationship between the density of red squirrel populations and snow-tracks is not known (but see Stephens et al. 2006 and Jousimo & Ovaskainen 2016 and references therein for a method for converting snow-track density to density of animal populations), but the red squirrel track density correlates positively with the number of litters (Selonen et al. 2015). Chapter **III** focuses on the spatial synchrony in red squirrel populations and the effects of top-down and bottom-up regulators on year-to-year fluctuations, whereas in Chapter **IV** the focus is on documenting a long-term trend and identifying underlying reasons. In Chapter **III**, I studied the relative effects of predators, the pine marten (*Martes martes*) and the northern goshawk (*Accipiter gentilis*, hereafter goshawk), and food availability, on the red squirrel snow-track density, while also taking into account the weather of the census day and the coarsely classified habitat type of the census site. In Chapter **IV**, I calculated regional population growth rates of the red squirrel from extensive snow-track data from Finland and Russia from a period of 17 years. I also aimed at explaining the change in the red squirrel abundance, as measured with the population growth rate, with the simultaneous changes in various possible explanatory variables, including climate, predators, food availability, and forest cover. Here, a special interest was whether the ongoing global warming, which has affected the abundance and area of distribution of numerous animals (reviewed in e.g. Walther et al. 2002, Parmesan 2006), has had some effect on red squirrel populations.

In this thesis, I aimed at answering the following research questions:

- 1) How do the partially conflicting needs to avoid predators and to settle in a high-quality habitat shape the occupancy patterns of
 - a. the flying squirrel
 - b. the red squirrelin a fragmented, heterogeneous landscape? (**Chapter I**)

- 2) How does the red squirrel sex ratio vary in space and time, and can a bottom-up effect explain it? (**Chapter II**)

- 3) What is the range of spatial synchrony in changes in the red squirrel abundance in Finland? (**Chapter III**)
- 4) What are the relative contributions of food availability and predator density on
 - a. the variation in the red squirrel density from year to year and on a small spatial scale (**Chapter III**)
 - b. the long-term change in populations over a larger spatial scale? (**Chapter IV**)
- 5) Is the red squirrel affected by the ongoing global warming? (**Chapter IV**)

For 1a and 1b in Chapter I, I predicted the nest box occupancy by flying squirrels and red squirrels to be lower where the predation risk index is higher, and the occupancy to increase with the increasing area of a high-quality habitat surrounding nest boxes. In addition, I anticipated that there can be interactive effects between different kinds of habitats and the predation risk on the nest box occupancy, which would indicate trade-offs (in high quality habitats) or habitat specific predation. For the red squirrel, I predicted the occupancy rate of the nest boxes in spruce forests to be high in years with an abundant spruce cone crop and that in pine forests to be high in spruce cone crop failure years. In Chapter II, for question 2, my prediction was that the cone crop explains at least some of the variation in the red squirrel sex ratio. Of course, I also assumed the sex ratio variation to be seen in the data, because this was already shown by Lampio (1965). In Chapter III, I expected synchrony to occur between at least close sites (question 3), and the red squirrel snow-track density to be strongly positively associated with the spruce cone abundance and negatively associated with the predator abundance (4a). Finally, for study question 5 assessed in Chapter IV, I expected that the red squirrel might have increased in the northernmost parts of its range as a response to global warming, because warming might increase cone crops and overwinter survival (4b).

2. MATERIALS AND METHODS

2.1 The study species

2.1.1 *The Eurasian red squirrel*

The red squirrel is one of the two squirrel species in Finland, the other being the Siberian flying squirrel. The red squirrel is common throughout the country up until the forest line, and is probably the most commonly observed wild mammal because it is diurnal and thrives near human settlement. In the 20th century and earlier, it was also an important game mammal in Finland, and red squirrel hunting provided an extra income for many Finnish families until the 1960s. Hunting was so intense in the 1920s and '30s that in some years the total catch was over 2 million, and in some years the hunting had to be prohibited to allow for the populations to recover from overexploitation. Nowadays, red squirrel hunting is a rare hobby, and the yearly catch is between 3000 and 10000 individuals (Riistaweb 2018, Luke 2018a). Although no estimate of the size of the red squirrel population exists, the small number of individuals hunted is thought to have no effect on the population.

The red squirrel's area of distribution covers most of Eurasia, extending from Ireland and Spain in western Europe to Japan and the Kamchatka Peninsula in the east (Lurz et al. 2005). In boreal coniferous forests, such as in Finland, conifer seeds are the main food resource for most of the year, although red squirrels opportunistically eat many kinds of food, from various kinds of plant material, fungi and invertebrates under natural conditions to human food in cities (reviewed in Lampio 1967, Lurz et al. 2005, Krauze-Gryz & Gryz 2014, Andrén & Lemnell 1992, V. Selonen pers. comm.). In Finland, spruce seeds are preferred, but pine seeds are also consumed, especially when the availability of spruce seeds is low. If there is shortage of both spruce cones and pine cones during winter, the red squirrel feeds on spruce buds. Spruce cones mature in autumn and provide a food resource for red squirrels until the next spring, when the seeds fall, but the level of the cone crop shows remarkable year-to-year variation (Farjon 1990). A good cone crop in the preceding autumn and winter correlates with a higher abundance of the red squirrel in spring and summer, both due to increased overwinter survival and reproductive success (Andren & Lemnell 1992, Wauters et al. 2008, Selonen et al. 2015). Some studies also suggest an immediate or anticipatory response, whereby red squirrels in southern and central Europe reproduce more when the coming spruce cone crop in the same autumn will be abundant (Boutin et al. 2006, Wauters et al. 2008). As their wide range suggests, red squirrels can utilize many types of forested habitats from temperate broad-leaved to boreal coniferous woodlands and also parks and other human-modified green spaces within (semi-)urban areas (Magris & Gurnell 2002, Lutz et al. 2005). Red squirrels build dreys (twig-nests) in trees but also utilize nest boxes provided by humans.

The red squirrel is prey for both mammalian and avian predators. The most common predators under natural conditions are the goshawk and the pine marten, of which the former is clearly more important, but in suburban and urban areas, also foxes (*Vulpes vulpes*) and especially cats (*Felis catus*) can hunt red squirrels that move on the ground (e.g. Kenward et al. 1981, Halliwell 1997, Penteriani 1997, Magris & Gurnell 2002, Randler 2006, Fey et al. 2016). Red squirrels are considered to be more important for their predators when other prey, like smaller mammals, are scarce (Widén 1987, Korpimäki et al. 1990, De Marinis & Masseti 1995). In most communities, they are not the main prey for any predator, but occur in small proportions in the diets of many predators. From the red squirrels' point of view, predation does not seem to suppress their numbers in most systems (Petty et al. 2003, Sheehy et al. 2014, reviewed in Sheely & Lawton 2014, but see Halliwell 1997, Selonen et al. 2016).

Red squirrel females can produce two litters during the reproductive season. The first litter is born in spring (March–April) and the second one in summer (starting from May; Wauters & Lens 1995, Selonen et al. 2015). Each litter has 1–6 offspring, the mean litter size being around 3 (Wauters & Lens 1995, reviewed in Lurz 2005; see Mari et al. 2008 for the record litter size of 7). The young are weaned when 8–10 weeks old, once they have been moving outside the nest and eating solid food for a few weeks (reviewed in Lurz 2005). Females can reproduce when 1 year old, and based on a study on Belgian red squirrels, the average lifetime reproductive success of females who successfully reproduce at least once is around 5 (Wauters & Dhondt 1995).

2.1.2 The flying squirrel

The flying squirrel is a nocturnal arboreal squirrel, whose range extends from Finland to Japan (Wilson & Reeder 1993). In Finland, it has suffered from habitat loss, fragmentation, and degradation (Hokkanen et al. 1982, Hanski et al. 2001, Lampila et al. 2009, Rassi et al. 2010, Selonen et al. 2010, Koskimäki et al. 2014), and has been previously classified as vulnerable, but was classified as near-threatened in the latest Red List (Rassi et al. 2010, Liukko et al. 2016). It is protected under the EU Habitats and Species Directive, which means that the resting and reproduction sites of flying squirrels should be protected.

The flying squirrel is strictly herbivorous compared to the rather omnivorous red squirrel. Flying squirrels mainly eat leaves (in summer) and catkins (in winter) of deciduous trees, preferring aspen (*Populus tremula*), alder (*Alnus incana* and *A. glutinosa*) and birch (*Betula pubescens* and *B. pendula*), but also conifer buds, berries and lichen in smaller amounts (Airapetyants & Fokin 2003, Hanski et al. 2000, Hanski 2016). They nest in cavities made by woodpeckers or in old red squirrel dreys and also readily accept nest boxes made by humans. The main predators of the flying squirrel are the Ural owl (*Strix uralensis*) and the northern eagle owl (*Bubo bubo*), the former being more important. Also goshawks can kill flying squirrels, although they are mostly active at different times of the day. In spring and summer, during mating season and when the

females have offspring, respectively, flying squirrels are also active in daytime (Airapetyants & Fokin 2003, Hanski 2016), facing increased predation risk from diurnal predators, such as the goshawk.

Although flying squirrels rely on deciduous trees for food and nesting cavities, they prefer mature and old mixed forests as their habitat (Hanski et al. 1998, Santangeli et al. 2013). It is considered that old spruces provide them with shelter, both from predators and from harsh weather, and that spruce branches are the most suitable for flying squirrels' catkin storages (Hanski 2016).

2.2 Study areas

All the work presented in Chapters I–III was conducted in Finland, whereas in Chapter IV, in addition to Finland, parts of north-western Russia are included. The main vegetation type within the study areas is boreal forest.

In Chapter I, the study area is situated in the municipality of Kauhava, western Finland (62° 54'–63° 16' N, 22° 54'–23° 47' E). There are nest boxes distributed over an area of over 900 km². The landscape is characterized by a mosaic of agricultural areas and forests, of which the majority are commercially managed. The area also features some peatlands and forests in a more natural state. The study area is relatively sparsely populated, and the settlement mostly consists of farm houses and other detached houses.

In Chapter II, which deals with old hunting data by Lampio (1965), most of the skins came from the southern half on Finland (roughly south of Oulu, 65° N), but some from as far in the north as Kittilä and Inari (up to 68° 59' N). Chapter III covers most of Finland, excluding most of the archipelago and the very northernmost tundra areas in Lapland, where spruce does not grow and, hence, there are no established red squirrel populations.

Chapter IV extends the study area to north-western parts of Russia, roughly from 56° to 69° N in latitude and from 20° to 60° E in longitude, covering about 1 000 000 km². The study area hence extends from western Finland to west of the Ural Mountains.

2.3 Squirrel data

2.3.1 Snow-track censuses

Finland has a long tradition of game animal monitoring. As early as in the 1940s the populations of the most hunted prey species were estimated based on a network of field observations. The snow-tracks of all game mammals, including the red squirrel, have been censused in Finland since 1989. Even though the red squirrel is an arboreal animal, they do move on the ground often (even most of their time in late winter) to search for their previously scatter-hoarded food items (Kenward & Tonkin 1986, Wauters et al. 2002) and also to move from tree to tree. The snow-track censuses are conducted by

skiing or walking the same triangular census lines every year and counting and identifying snow-tracks that cross the transect line.

There are two types of triangles in two land-use types: wildlife triangles in forested areas and field triangles in mosaic-like agricultural areas. Wildlife triangles are more numerous and they have been censused since 1989, whereas field triangles were established in 1999 and most of them are situated in southern and western Finland. The lengths of all sides of a wildlife triangle are 4 km, making the total length of census line in each triangle 12 km. The respective values for field triangles are 2 and 6 km. Wildlife triangles are by definition established in forested areas; however, if the forest is managed or clear cut, the triangle is continued to be censused. Intensive forest management is common in Finland and therefore the inclusion of clear-cut areas, and later sapling stands, is considered to make the results realistic. If only triangles in more pristine forests were censused, the results would be biased and could not be used to estimate animal densities in the landscape in general. Field triangles, on the other hand, are situated in agricultural areas among the mosaic of fields, forest patches and human settlement, which is typical of southern and western Finland. As per guidelines, about half of the transect line runs through fields and the rest can be in other human-altered areas and natural habitats, like forests (Luke 2018b). There have been about 1900 wildlife and field triangles during the 30 years of census history but less than a thousand are censused per year, and some triangles have been abandoned while new ones have been established. In some winters in the 2010s there has not been adequate snow cover to conduct censuses in parts of southern Finland.

The censuses are made in January–March within 1–2 days after snowfall, when new snow has covered or erased all previous snow-tracks. Alternatively, a pre-census is made during which all tracks are covered or marked, so that in the actual census the new tracks can be distinguished from the old ones, and this way the time over which the tracks have accumulated is known. In Chapters III and IV, I only used triangles that had a collection time of 1 day, because it was uncertain whether tracks accumulate linearly over longer times.

Snow-track censuses in Russia are made in a quite similar fashion. On the day before the actual census, old tracks are marked or wiped out, and the next day new tracks (for which accumulation time = 1 day) crossing the transect line are counted (Bragina et al. 2015). The transects can take any form, i.e. they are not necessarily triangular as in the Finnish system, and the length of individual transect lines varies from 8 to 12 km (Bragina et al. 2015, J. Kurhinen pers. comm.). Tracks are tallied by species and habitat (Bragina et al. 2015). To make the data match the Finnish wildlife triangles, I only used data from forests. The part of the data that I had access to, through collaborators, covers years from 1996 to 2012.

2.3.2 Nest box occupancy

In Chapter I, I studied the red squirrels' and the flying squirrels' nest box occupancy in a long-running study system in the Kauhava area, where Erkki Korpimäki and colleagues have established a network of over a thousand Tengmalm's owl (*Aegolius funereus*) and Pygmy owl (*Glaucidium passerinum*) nest boxes (e.g. Korpimäki 1986, Suhonen et al. 2007, Korpimäki et al. 2011, Morosinotto et al. 2016). Pygmy owl boxes have an entrance-hole of 45 mm in a front wall that is >50 mm thick, and the boxes are made of whole tree trunks to resemble natural cavities. There are two Pygmy owl nest boxes per site, 80–100 m apart, because these nest boxes are also used by flying squirrels, and this set-up ensures their availability for both species. Tengmalm's owl nest boxes are made either from board or from tree trunk and they have a wider entrance hole of 80–100 mm. This box type is used by red squirrels in addition to the Tengmalm's owls, and they are distributed singly in the landscape with the density of approximately 1 nest box/2 km². The density of Tengmalm's owls is rather low in the study area, and therefore there is little competition for nest boxes between owls and red squirrels. Both box types are checked at least once every spring. I used data from 1999 to 2015 for the red squirrel and from 2002 to 2015 for the flying squirrel, and in the case of multiple visits per nest box during the same spring, I only used the outcome (presence/absence of signs of squirrel inhabiting the box) of the first check to ensure equal search effort, and hence detection probability, between nest boxes.

2.3.3 Sex ratio data

The sex ratio data that I re-analysed in Chapter I were originally collected and published by Teppo Lampio (1965). In the first half of the 20th century, red squirrels were hunted for their fur, and the pelts were tagged to keep information on their origin. This practice is what enabled Lampio to collect a data set that covers most of Finland by visiting fur stores in Helsinki. In practice, he sexed 187 404 skins based on the distance between the anus and urinary opening and the presence or absence of a penis scar. At the time, red squirrels were hunted in November and December, but nowadays the hunting season is longer, from the beginning of November to the end of February (Lampio 1965, The Finnish Wildlife Agency 2018). Because hunting took place outside of reproductive season, Lampio (1965) argued that shooting probability did not differ between the sexes. The timing also means that the calculated sex ratio (proportion of males of all samples) is not an estimate of pure adult sex ratio, but emerges from the sex ratios of juveniles, born in the same year, and adults. The skins of male and female red squirrels do not differ in quality or value, so there is no reason to suspect that either would have been sold more quickly, which would have biased the sex ratio observed in a fur store from that in the original sample. There are data for years 1946, 1948–1950, 1952–1954, and 1963. In 1947 and 1951, hunting was not allowed because the red squirrel population was estimated to be too low, and was left to recover from the preceding overexploitation.

2.4 Explanatory variables

Red squirrels in boreal coniferous forests are heavily dependent on spruce seeds as their main food resource (e.g. Lampio 1967, Andren & Lemnell 1992, Lurz et al. 2005). Therefore, I took the spruce cone crop into account in some way in all the chapters. Because spruce cone crop is mostly determined by temperature (Pukkala et al. 2010) and is consequently strongly spatially autocorrelated within hundreds of kilometers (e.g., Ranta et al. 2010, Zamorano et al. 2018), the spruce cone crop values and the red squirrel data do not need to originate from exactly the same place for analysing purposes.

In Chapter **II**, which concerns the 1940s, '50s and '60s, I used estimates of the level of cone crop that were published in the Finnish forestry magazine *Metsälehti*. Information on the level of cone crop was, and still is, of importance to forestry personnel and forest owners, because it affects the natural recruitment of new seedlings, and because cones can also be collected and sold to tree nurseries for some extra income. The estimates of cone abundances were published as verbal descriptions and maps. I georeferenced and digitalized photographs of the maps to link the cone crop estimates to local estimates of red squirrel sex ratio. For the last two years, 1952 and 1963, I used data from the archives of the Finnish Forestry Research Institute (later Luke). Both the published maps and the later estimates were based on counting cones in research forests and on professional views on the level of local cone crop in each year. For Chapters **I**, **II**, and **IV**, I used cone crop estimates from Luke's research forests, where the number of cones per tree is counted yearly. In Chapter **I**, considering the Kauhava area, I used estimates from the three nearest research forests within ca 75 km from the center of our study area. In Chapter **III**, I interpolated the cone crop values over Finland and intersected interpolated values at census triangle locations. In Chapter **IV**, the cone crop was only used in a descriptive way in supplement because of the scarcity of the data from Russia. Instead, I used the change in summer temperature (May-Sep) as a proxy for the possible change in the level of cone crop, because there is strong correlation between temperature in previous growing season and the cone crop (Pukkala et al. 2010).

In Chapters **I**, **III** and **IV**, I also studied the effects of predators. In Chapter **I**, I used goshawk data (for both the flying squirrel and the red squirrel) and Ural owl data (for the flying squirrel only) that originate from long-term studies carried out in the study area. For both predators, I modelled the strength of their presence in the landscape based on their nest locations, assuming predation risk for squirrels to be the highest close to the predator nest and to decrease with increasing distance from the nest following a flat-top Gaussian kernel. The resulting predation risk index value was intersected for every nest box location to describe predation threat for squirrels at that site. In Chapter **III**, I used the same method for the whole Finland and intersected modelled goshawk risk index values at census triangle locations. In Chapters **III** and **IV**, estimates of pine marten density were based on the same Finnish and Russian snow-track censuses as the red squirrel data.

In Chapters **I**, **III** and **IV** I took into account some environmental variables. To study the habitat use of squirrels under varying predation risk in Chapter **I**, I utilized maps that had been made of the study area combining different remote sensing data sources (Morosinotto et al. 2017). I calculated standardized amounts of different land-use classes or habitat types within small and large buffers from the squirrel nest boxes using ArcGIS and R (R Core Team 2016). The sizes of the buffers were chosen so that the smaller buffers include home-ranges and the larger buffers roughly correspond to dispersal distances. In Chapter **IV**, I used the loss of forest canopy cover (Hansen et al. 2013) as a proxy for deforestation and habitat loss. This global forest cover loss data has a spatial resolution of 1 arc-second and consists of binary values for canopy cover loss occurring (1) or not occurring (0) within a pixel during 2000–2014. For a rough estimate of deforestation within each study region, I used the mean value (0-1) of pixels within that area. Finally, in Chapters **III** and **IV**, I used weather data to account for census conditions (**III**) and to study the effects of global warming on the red squirrel (**IV**). These weather data were provided by the Finnish Meteorological Institute (FMI) and All-Russian Research Institute of Hydrometeorological Information – World Data Center (WDC RIHMI). In Chapter **III**, I extracted the temperature and precipitation values for each census triangle and day from interpolated maps, and in Chapter **IV**, I used data from the weather station closest to the center of each study region to calculate changes in climatic parameters over the 17-year study period.

2.5 Statistical methods

In Chapter **I**, I used binomial generalized linear mixed models to study the effects of predation risk and habitat type on the nest box occupancy by squirrels. Following the assessment of multicollinearity in the data with variance inflation factors (VIFs), I analysed the effect of young pine forest in a separate model due to its large VIF. The nest box ID and the site ID were set as nested random factors in the flying squirrel occupancy models and the site ID as a single random factor the in red squirrel models, reflecting the spatial configuration of the two nest box types in the study area.

In Chapter **II**, I grouped the data into 50×50 km cells and assessed the autocorrelation of the red squirrel sex ratios in these cells using Moran's I (Moran 1950, Bjørnstad et al. 1999a). Here, I focused on the years 1949, 1950, and 1952, for which there were sufficient data ($n > 50$ cells) for this kind of a spatial analysis. To study whether the abundance of cones could explain variations in the sex ratio, I used a linear mixed model with year as a random factor. All years were used in this analysis.

The Chapter **III** is a collaboration with statistician Jussi Jousimo, who has specialized in modelling challenging ecological data, such as track densities. Here, we analysed spatial synchrony in red squirrel snow-tracks using Moran's I, and studied the effects of predators, food and weather on the red squirrel using an integrated nested laplace approximation (INLA; Rue et al. 2009) and a spatio-temporally explicit hierarchical Bayesian model (Cameletti et al. 2013, Jousimo & Ovaskainen 2016) with a spatio-

temporal random term and the triangle length as an offset term. Models with different combinations of explanatory variables and with and without the spatio-temporal random term were compared with Watanabe-Akaike information criterion (WAIC; Watanabe 2010).

In the last chapter (**IV**), I first calculated the regional population growth rate and then related that to simultaneous regional changes in the red squirrels' food availability, predator density, habitat availability and climate. Here, the regions were approximately 1 degree latitude \times 2 degrees longitude in size. The population growth rate per region over 1996–2012 was modelled with a hierarchical state-space model (Kéry & Schaub 2012) which allowed for spatial correlations between neighboring regions. The effect of changes in the possible explanatory variables on the calculated red squirrel population growth rate was studied with a linear model. All the analyses in Chapters **I-IV** were done using the R programming environment (R Core Team 2016).

3. RESULTS AND DISCUSSION

3.1 The effect of predators and habitat on nest box occupancy by arboreal squirrels

The results of Chapter I show that the predation risk landscape affects the spatial occurrence of both the flying squirrel and the red squirrel (Fig. 1A, B). Especially the nest box occupancy of flying squirrels was lower close to the nests of their main avian predator, the Ural owl. Also red squirrels were negatively affected by their main avian predator, the goshawk, but the result was not as clear as that for flying squirrels. The expected preferred habitat types, i.e. mature and old mixed forests for the flying squirrel and mature and old spruce forest for the red squirrel, were not significantly associated with the nest box occupancy in this study. In contrast, agricultural areas had a positive effect on both species based on both small and large scale models, i.e. within 200 m and 1 km from nest boxes for the flying squirrel and within 300 m and 2.5 km for the red squirrel (Fig. 1C, D). For the flying squirrel on both scales and for the red squirrel on the smaller scale, there was a threshold after which the effect of increasing area of farmland turned negative. Red squirrels were also positively associated with built areas on the smaller scale, indicating a positive effect of human settlement on the red squirrel. Young pine forest affected the occurrence probability of both squirrels negatively, and in addition, there was a significant interaction between the area of young pine forest and a goshawk risk index on red squirrels. Other tested interactions between predators and high or low quality habitat types were not significant. The nest box occupancy of flying squirrels increased during the study period 2002–2015, whereas that of red squirrels decreased during 1999–2015.

The results show that predators have a detrimental effect on the nest box occupancy of both the flying squirrel and the red squirrel. Lower occupancy rate closer to predator nests can be due to avoidance of these sites by the squirrels, predation on individuals who settle there, or both. Whichever the mechanism, the results suggest that erecting nest boxes for Ural owls in or close to flying squirrel territories should be carefully considered in order to conserve the flying squirrel. This is because there is a shortage of natural cavities in the Finnish forests, and therefore the nest boxes have a great impact on where Ural owls settle. The results of Chapter I concerning the effect of the Ural owl on the flying squirrel are consistent with previous studies. Byholm et al. (2012) showed how flying squirrels avoid Ural owl nests, and even sought protection from Ural owls by settling near goshawk nests. No similar association with goshawks was seen here.

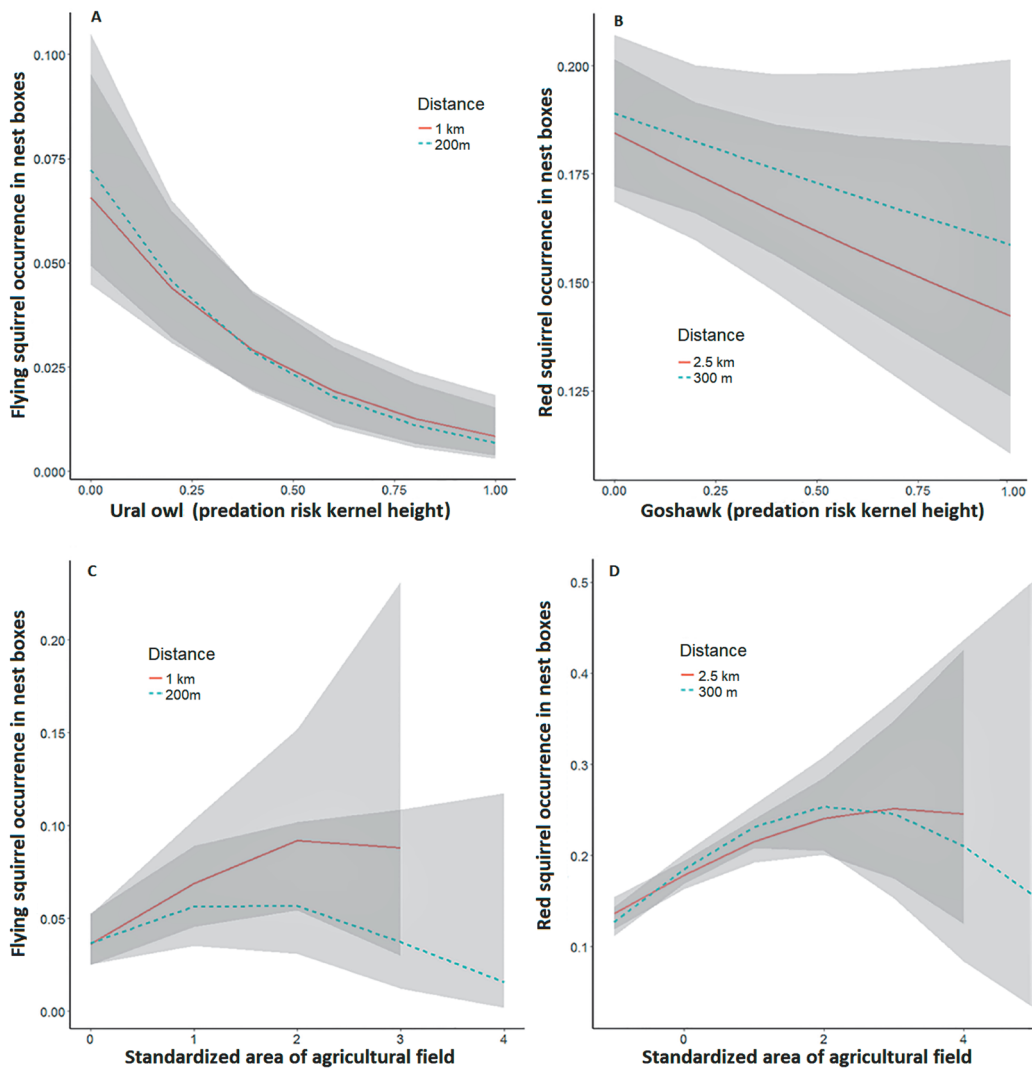


Figure 1. The main avian predators decrease and agricultural areas increase the nest box occupancy by arboreal squirrels. The effect of A) the Ural owl on the flying squirrel, B) the goshawks on the red squirrel, C) agricultural areas on the flying squirrel and D) on the red squirrel based on small (blue dashed line) and large scale models (red line).

Also, the negative impact of predation by the spotted owl (*Strix occidentalis*) on the northern flying squirrel (*Glaucomys sabrinus*) in North America is seen on population level, at least in some systems (Forsman et al. 1984, Carey et al. 1992). For the red squirrel, the fact that goshawks had a negative impact based on one model but not the other, suggests that there is some effect, but that the relationship is not very strong. The significant interaction between young pine forests, a strongly non-preferred habitat, and goshawk risk index, further suggest habitat specific predation. This makes sense because after thinning young pine forests are light and sparse and thus provide good visibility as well as hunting space for large avian predators. In contrast, there was no obvious

indication of a trade-off between the predation pressure and settling in a high-quality habitat for either species, as indicated by the non-significant effects of other interaction terms. Admittedly, interpreting this results is made more difficult by the fact that the squirrels in this study did not show statistically significant preference towards the mature and old spruce-dominated (for the red squirrel) or mixed (for the flying squirrel) forests that they generally prefer (e.g. Hanski et al. 1998, Delin & Andrén 1999). It is possible that the habitat type classification that I used does not fully capture characteristics of the forest important for squirrels, like density of forest (Summers & Proctor 1999, Flaherty et al. 2012). Previous studies on the relationship between the red squirrel and the goshawk have yielded somewhat conflicting results but mostly support a view that red squirrels are important in goshawk diet, but that predation by goshawks does not affect the population dynamics of the red squirrel. In the same study region in Kauhava, Finland, Selonen et al. (2016) showed avian predators to decrease the red squirrel snow-tracks during winter with a low cone availability, whereas another winter-time study in Finland found no effect of goshawks (Jokimäki et al. 2017), and the analysis of the Finnish snow-track data revealed a positive association, even considering different time-lags (Chapter III). It seems that the predation pressure in most cases is not so strong that it would suppress red squirrel numbers on population level, although it is clear that goshawks do commonly prey on red squirrels (e.g. Penteriani 1997, Kenward et al. 1981, Gurnell 1983, Widén 1987, Petty et al. 2003 and references therein, Tornberg et al. 2006, Selonen et al. 2010).

The lack of effect of amount of preferred habitat on nest box occupancy may suggest that both red squirrels and flying squirrels can be flexible in their habitat use, when nest sites (i.e. nest boxes in this study) are not a limiting factor. Also, some previous studies have concluded that arboreal squirrels can behave rather as habitat generalists than specialists under some conditions (Magris et al. 2002, Wheatley et al. 2005, Hoset et al. 2017), but also a plethora of studies show clear habitat preferences and requirements (e.g. Delin & Andrén 1999, Selonen et al. 2001, Santangeli et al. 2013). It may be that these were not detected in this study because of methodological reasons like habitat classification, or more likely, because most forest types where boxes are put are of good enough quality. The increasing trend of flying squirrels suggests that their populations can survive and even increase in a rather fragmented landscape with low proportion of old-growth forests (7 % of total land area within the buffers around nest boxes, and less of the landscape in general), when nesting sites are not a limiting factor. Fragmentation has been found to affect flying squirrels negatively in previous Finnish studies (Mönkkönen et al. 1997, Reunanen et al. 2002, but see Santangeli et al. 2013, Selonen & Hanski 2014). The declining trend in the red squirrel, as suggested by decreasing proportion of occupied nest boxes and the results of Chapters III-IV, is discussed in 3.3 and 3.4.

Interestingly, I found both squirrel species to occupy nest boxes more likely if there was agricultural land nearby. Open fields are obviously an unsuitable habitat for arboreal

squirrels, so I assume this result to arise from the effect of forest edges rather than fields *per se*. Trees growing on forest edges get ample light and may be situated on more fertile soil, which may increase their productivity and nutritional value. Indeed, conifers produce more cones at forest edges than inside forest (Phillipson 1987). Squirrels are known to selectively forage in particular trees or on particular food items, presumably because of differences in nutritional values (Moller 1986, Schmidt et al. 1998, Molinari et al. 2006). Also Santangeli et al. (2013) found flying squirrels to prefer open areas and concluded that that is most likely caused by deciduous trees growing under good conditions near forest edges. I assumed that there must still be an upper limit for the proportion of open areas within the home range of arboreal squirrels, and indeed, the quadratic term for farmland was significant in the small scale models for both species, and for flying squirrels, also in the large scale model. The nest box occupancy of flying squirrels increased with increasing area of farmland up until about 50 % of the surrounding landscape was open, after which the occurrence probability decreased. The red squirrel, on the other hand, seemed to tolerate or favor an even greater proportion of fields, up to as much as 70 % of the landscape. Also Dylewski et al. (2016) found red squirrels to prefer sites close to forest edges and ascribe this result to the higher cone production of large trees near open areas.

The red squirrel occupancy probability also slightly increased close to built areas. In the land use classification used here, the land use class ‘built’ comprises of roads, mines (of which there were few within the study area, and these were sandpits), and all kinds of buildings. Also a previous study in Finland found red squirrels to be more abundant close to urban areas (Jokimäki et al. 2017, see e.g. Babińska-Werka & Żółw 2008 for urbanization of red squirrels elsewhere) and argued that it is due to supplementary feeding provided by humans. Supplementary feeding has been observed to benefit red squirrels (e.g. Magris & Gurnell 2002, but see Krauze-Gryz & Gryz 2014). Feeding birds, and practically inevitably also red squirrels, with sunflower seeds, peanuts and oats is popular in the Finnish countryside and is a likely explanation for the red squirrels’ preference for built areas also in this study. It is worth noting that built areas in our study area are not very urban by global standards but consists mostly of farms and other detached houses, often with gardens that can provide red squirrels with food even when no bird-feeding takes place.

Finally, I found partial support for the effect of food availability on the nest box use: red squirrels occupied nest boxes with more spruce forest around them when spruce cone crop was good but did not use nest boxes with more pine forest when the spruce cone crop was low. I expected a shift from spruce- to pine-dominated forests to occur when the spruce cone crop had failed. Previous studies have demonstrated how red squirrels utilize different kinds of patches within their home range and also occasionally move to a new home range following changes in food availability (Lurz et al. 2000, Di Pierro et al. 2011). It seems that in our study area, red squirrels are attracted to spruce-dominated

sites when they provide ample food, but in years with a low spruce cone crop do not particularly favor pine-dominated patches.

In summary, to answer the questions stated in The aims of the thesis, I found in Chapter I that both flying squirrels and red squirrels are negatively affected by their main avian predators, but did not find support for a trade-off between predator avoidance and settling in a high-quality habitat. Hierarchical habitat selection, whereby animals avoid predators on large scale but choose habitat based on also other limiting factors on smaller scale (Rettie et al. 2000, Dussault et al. 2005), may explain why squirrels were clearly negatively affected by a predation risk landscape but still apparently did not have to compromise habitat selection. Based on the results, both the flying squirrel and especially the red squirrel seem to tolerate fragmentation within an agricultural landscape. The results also hint that flying squirrels do not necessarily need continuous old forests, if nest boxes are available in all kinds of forests. However, young pine forest was found to be an especially unfavorable habitat for both species. Lastly, the clear detrimental effect of Ural owls on the flying squirrel nest box occupancy begs for careful consideration on where nest boxes for Ural owls should be erected. My recommendation is to not put nest boxes for Ural owls closer than, for example, 2 km from known or highly potential flying squirrel territories in order to conserve the near-threatened flying squirrels.

3.2 Variation in the red squirrel sex ratio

The re-analysis of data on 187 404 red squirrel skins (Lampio 1965) revealed that the red squirrel sex ratio (proportion of males of all individuals) deviated significantly from an equal sex ratio, 0.5, in 28 % of the studied 50 × 50 km grid cells (Fig. 2). The bias occurred more often towards males (19 % of cells) than towards females (8 % of cells). In 73 % of the 283 grid cells the sex ratio did not deviate significantly from parity, and the proportion of males over all years and all regions was 50.9 %. This result is statistically significantly different from 50 % due to the large sample size, but I do not consider that as an ecologically important bias. However, the yearly variations are marked and interesting. The bias in the sex ratio showed large-scale spatial synchrony: areas up to 200 km across showed bias towards the same sex. The areas with a deviating sex ratio were not constant between years, and a cell that had a male-biased sex ratio in one year could have a female-bias or no significant bias in the next year. My hypothesis, that the variation in the cone crop could drive the variation in the red squirrel sex ratio (Trivers & Willard 1973, Ranta et al. 2010), was not supported.

The results of Chapter II add to the evidence that biased sex ratios sometimes occur in squirrels (Pulliainen 1982, Lurz 1995 cited in Lurz et al. 2005 on Eurasian red squirrels; on other squirrel species Hurly 1987, Michener 1989, Millesi et al. 1999, Sherman &

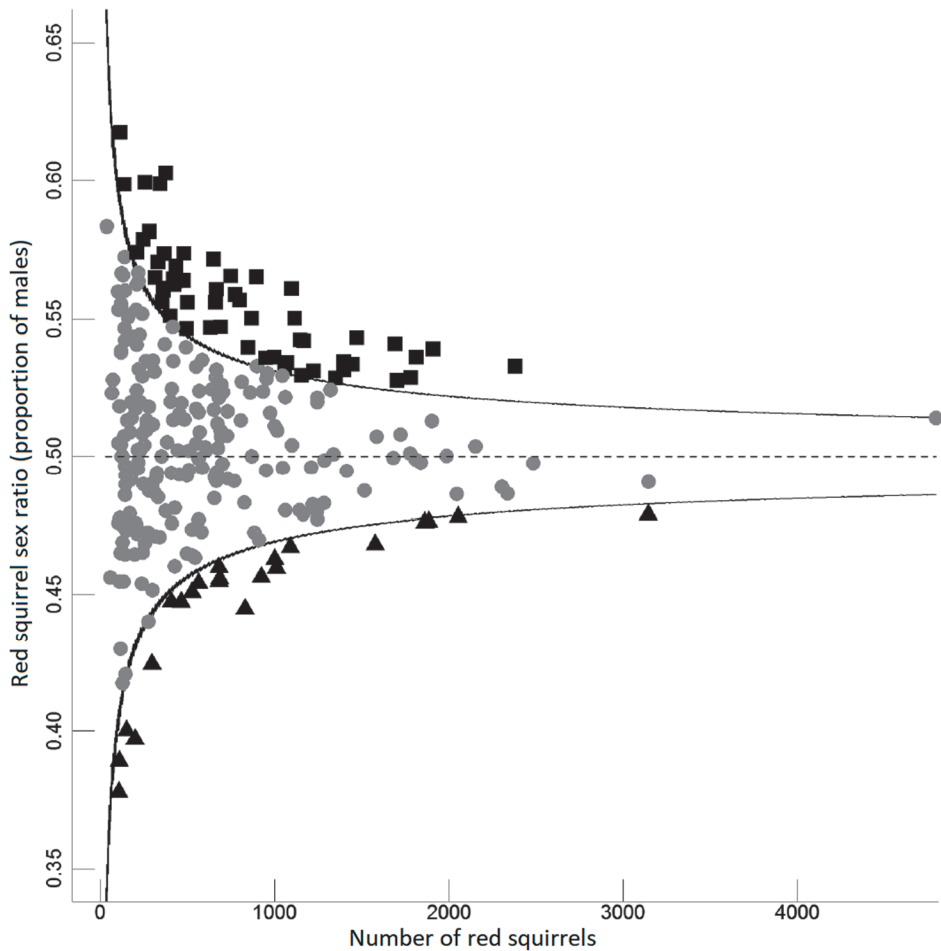


Figure 2. A funnel graph of the annual red squirrel sex ratio plotted against the sample size (the number red squirrel skins that were sexed in a 50×50 km grid cell). Dashed line: equal sex ratio of 0.5. The funnel indicates the 95 % confidence interval. Grid cells falling outside the funnel thus deviate more from parity than expected by chance. Black squares above the funnel: significant male bias. Black triangles below the funnel: significant female bias.

Runge 2002, Kusahara et al. 2006, Gür & Barlas 2006, Ryan et al. 2011, but see Gedir and Michener 2014).

To my knowledge, this, naturally together with the original study by Lampio (1965), is the largest-scale study to show such variations in squirrel sex ratio. There are possible ecological consequences of a biased sex ratio. The polygynous–promiscuous mating system of red squirrels (Lurz et al. 2005), in which the highest quality males account for most of the matings (Wauters et al. 1990), may lead to intensified male-male competition under a male-biased sex ratio and, therefore, increase the average quality of males who sire offspring. This may benefit females and the offspring but decreases mating success for lower quality males. On the other hand, when the sex ratio is biased towards females, the reproductive rate can decrease because an increasing female density leads to female-

female competition over the best core areas (Wauters & Dhondt 1992, Wauters et al. 2004).

While there are a number of factors that can affect the mortality of males and females differently, these are not likely to vary over time and space in such a way that they would produce spatiotemporal patterns in variations in the sex ratio like the ones documented here. For example, the mortality of male squirrels tends to be higher due to larger home ranges, greater moving distances, and the susceptibility to predation and traffic (Lampio 1965, Shuttleworth 2001, Wauters et al. 2001, LaMontagne et al. 2013), which should rather lead to a constantly slightly female-biased sex ratio than to a variable sex ratio. Therefore, it is difficult to envision a mechanism that would cause the sex ratio to vary in space and time through different mortality of the sexes. It seems more likely that the biases in sex ratio occur already at the time of birth, in contrast to emerging later in life through differing mortality rates. However, I found no support for the Trivers-Villard-hypothesis-driven prediction that resource availability could cause variation in the offspring sex ratio through variation in maternal condition (Trivers & Willard 1973). What, then, could have caused the spatiotemporally varying sex ratio? A possible mechanism is that suggested by Ranta et al. (2000) who showed that a Fisherian adjustment of the offspring sex ratio (Fisher 1930, Jennions & Kokko 2010) to the operational sex ratio (Emlen & Oring 1977) of the focal population and its neighbors can create spatial patterns in the sex ratio. It is plausible to assume red squirrels to adjust the sex ratio of their offspring, if they do that at all, to a local rather than a global operational sex ratio, because of obvious limitations of information on the latter. It remains possible that such a rather simple process drives spatial variations in populations (Bascompte & Solé 1995, Kareiva & Wennergren 1995, Ranta et al. 2000, Bjørnstad et al. 2002). The physiological mechanisms by which females can adjust the sex ratio of their offspring (reviewed in e.g. Cameron 2004, James 2008, and Navara 2010) are poorly understood in mammals and are beyond the scope of this thesis.

To answer the study question stated in The aims of the thesis, I found that the red squirrel sex ratio shows a large-scale spatial synchrony, as demonstrated with Moran's I correlograms, and that this bias occurred more often towards males. Moreover, the areas with either female- or male-biased sex ratios vary between years, but this variation was not due to variation in food abundance as measured with the level of spruce cone crop.

3.3 Spatiotemporal synchrony and drivers of fluctuations in red squirrel snow-tracks

Spatial range estimate in the best-fit spatiotemporal model for the Finnish snow-track data in Chapter III is 655 ± 90 km, which means that at this distance the spatial autocorrelation between red squirrel populations becomes negligible. Also the Moran's I correlograms show that changes in red squirrel track densities are synchronized over large spatial scales, and that this synchrony abates with distance through all distance classes, but the correlograms do not show where the populations become fully

disconnected on average as the negative synchrony appears to continue beyond the spatial coverage of the data. So both the correlograms and the spatio-temporal model suggest that synchrony of red squirrel populations occurs over very large distances. However, long range in the spatiotemporal model can also be an indication of spatial nonstationarity and should, therefore, be interpreted with caution.

The best-fit model for the density of red squirrel snow-tracks, based on model selection, included the covariates pine marten density, goshawk kernel height, spruce cone index, triangle type, precipitation, and temperature. Of these, pine marten, goshawk, cone index and temperature were positively associated with the red squirrel snow-track density. In contrast, precipitation and triangle type had negative effects, so that the red squirrel snow-track density was greater in field than in forest (i.e. in field triangles than in wildlife triangles). The estimated weights of the covariates reveal that the cone index has the strongest positive effect on the red squirrel density, whereas the triangle type has the largest absolute effect of all covariates. The 29-year time series revealed a decreasing trend in other parts of Finland, but an increasing trend in Southern Finland.

The estimated spatial range of synchrony in red squirrel populations is remarkably large for a small mammal. Methodological differences can hinder comparison of synchrony estimates between studies, which is why I also calculated Moran's I, a commonly used metric of spatial autocorrelation or synchrony, in addition to the spatial range estimate from the spatiotemporal model. Previous studies, where some sort of correlograms have been calculated from data on small rodents, have yielded estimates that are typically an order of magnitude smaller, being ca. 30–50 km (e.g. Steen et al. 1996, Bjørnstad et al. 1999b). However, red squirrels are arguably more mobile and disperse much further than, for example, voles (Lambin 1994, Lurz et al. 1997, Fey et al. 2016), which accounts for some of the range of the synchrony. Still, such a large range strongly hints on an underlying mechanism that also operates on a large scale. Indeed, a climate-driven synchrony can occur on a scale of hundreds of kilometers, or well up to 1000 km (e.g. Post & Forchhammer 2002). Abiotic factors, mainly temperature, which affect the cone crop, seem like a likely explanation for the synchrony in the red squirrel population fluctuations occurring on a scale of hundreds of kilometers. The simultaneous analysis of the effects of predators and food show a strong bottom-up effect with no indication of a top-down effect on population level. Of the possible mechanisms causing synchrony, i.e. dispersal (Ranta et al. 1995, Kendall et al. 2000), nomadic predators (Norrdahl & Korpimäki 1996, Korpimäki et al. 2005), trophic interactions with another species that also shows synchrony (Byholm et al. 2002, Satake et al. 2004, Cattadori et al. 2005), and the Moran effect (Moran 1953, Royama 1992), the two latest seem to be acting here. In other words, red squirrel populations are synchronized because weather, a type of Moran effect, causes their food resources to be synchronized over a large scale. Also Ranta et al. (1997) demonstrated how the Moran effect could lead to synchrony between red squirrel populations. Similarly, Kemp and Keith (1970) showed, based on fur records,

how the population fluctuations of the North American red squirrel (*Tamiasciurus hudsonicus*) are synchronized over vast areas due to food availability and weather.

Red squirrels were positively associated with both goshawks and pine martens, even when considering possible lagged effects, which were not included in the final model. This positive association of the red squirrel with both of the main predators suggests that shared habitat preferences drive their occurrence more than predator-prey interactions. Alternatively, it could be argued that the predators might have won the predator-prey space race (Sih 2005), because red squirrels need to settle in forests with enough mature coniferous trees that provide them with food, whereas the predators can settle where their prey are. On the other hand, the red squirrel is probably not such an important prey item that the predators would choose where to settle based on red squirrel densities. A suitable habitat in terms of food availability could, however, be viewed as a spatial anchor (Sih 2005) which forces red squirrels to settle where their resources are, regardless of possible predation risk. Also Sheehy & Lawton (2014) found the red squirrel and pine marten occurrences to be positively correlated but their study system is crucially different because of an alien species affecting the community. The study by Sheehy & Lawton (2014) was conducted in Ireland, where the invasive grey squirrel (*Sciurus carolinensis*) has replaced the red squirrel in many places, and the recovery of the red squirrel appears to be facilitated by pine martens preying upon grey squirrels more than red squirrels. The positive spatial association of the red squirrel with its predators is in concordance with earlier results that even though red squirrels sometimes form a substantial proportion of goshawks' and pine martens' diets, depending on the availability of other prey types (Widén 1987, Korpimäki et al. 1990, De Marinis & Masseti 1995, Penteriani 1997, Pulliainen & Ollinmäki 1996, Tornberg 2006, Selonen 2010), red squirrel populations are not suppressed by predation (Gurnell 1983 cited in Petty et al. 2003, Petty et al. 2003, Sheehy et al. 2014; but see Halliwell 1997). The popularity of the red squirrel as a game animal was partly based on the ability of its populations to recover quickly from heavy hunting, which also suggests that natural levels of predation are not likely to have a strong impact on its abundance.

There were more red squirrel tracks in the field triangles than in the wildlife triangles. Here, it has to be kept in mind that despite their name, the field triangles are not completely on fields, but by definition, about half of the census line should be on a field (25–75 %). The rest of the transect line crosses forests and human-altered areas, such as villages (Luke 2018b), because the very meaning of the field triangles is to survey animal populations in the mosaic-like landscape typical of southern Finland. The red squirrel snow-tracks in field triangles are in the forested parts and close to human settlement and not in the open field parts (J. Tiainen pers. comm.). As for example Jokimäki et al. (2017), Dylewski et al. (2016) and the results of Chapter I showed, the red squirrel can thrive close to forest edges and human settlement, which may explain a part of the high density of snow-tracks in the field triangles. The alternative food resources provided by humans can be important for the red squirrel, especially in those winters when the

availability of conifer seeds is low. Also the predators, the pine marten and the goshawk, do not normally occur as close to human settlement as the red squirrel, and indeed, the density of pine marten tracks was significantly lower in field than in wildlife triangles within the same area. Finally, the high density of the red squirrel in mosaic-like landscape is consistent with the view that red squirrels can tolerate moderate habitat fragmentation (Chapter I; reviewed in Selonen & Hanski 2014).

The weather of the preceding day was accounted for in the analyses, because it can obviously affect the accumulation of snow-tracks through changes in animal behavior. As expected, red squirrel tracks were more numerous when the preceding day had been warmer and less rainy. Also a number of previous studies have found similar results (Lampio 1967, Pulliainen 1973, Doebel & McGinnes 1974, Wauters & Dhondt 1987).

Interestingly, temporal trends varied between the Finnish provinces. Red squirrels appeared to have declined in other parts of Finland, but showed an increasing trend in Southern Finland (Fig. 3A). This is also the only province where both of the predators, the pine marten and the goshawk, have declined, and where the spruce cone crop is on average a little higher, although the average level of cone crop, too, has been slightly declining (Fig. 3B,C). This raises the question whether the predator guild as a whole would still have a suppressing effect on the red squirrel, at least locally. Nevertheless, and not mutually exclusively, same unidentified environmental changes may have favored red squirrels while decreasing the densities of its predators. One such environmental factor could be the urbanization in Southern Finland, where the human population is the densest and where it continues to concentrate more all the time. Red squirrels can do well in urban areas (Magris & Gurnell 2002, Babińska-Werka & Żółw 2008, Fey et al. 2016, Jokimäki et al. 2017, also Chapter I), whereas its predators vary in their state of adapting to urbanization. The pine marten is rare in Finnish cities, but the goshawk, while previously considered to prefer rural areas and to be poorly urbanized (Vuorisalo & Tiainen 1993, Vuorisalo et al. 2003) now occupies cities in southern Finland and even produces larger broods close to urban areas (Solonen 2008). However, the overall population trend of the goshawk has been declining in Finland, and it has been recently red-listed (Tiainen et al. 2015). Foxes and especially cats, which can be important predators in cities but not under natural conditions, on the other hand, are numerous in suburbs and cities. Also the fact that the red squirrel track density was higher in field triangles, situated mostly in southern and western Finland, supports the conclusion that the mosaic-like areas close to human settlement are favoured by the red squirrel, especially when natural food is scarce.

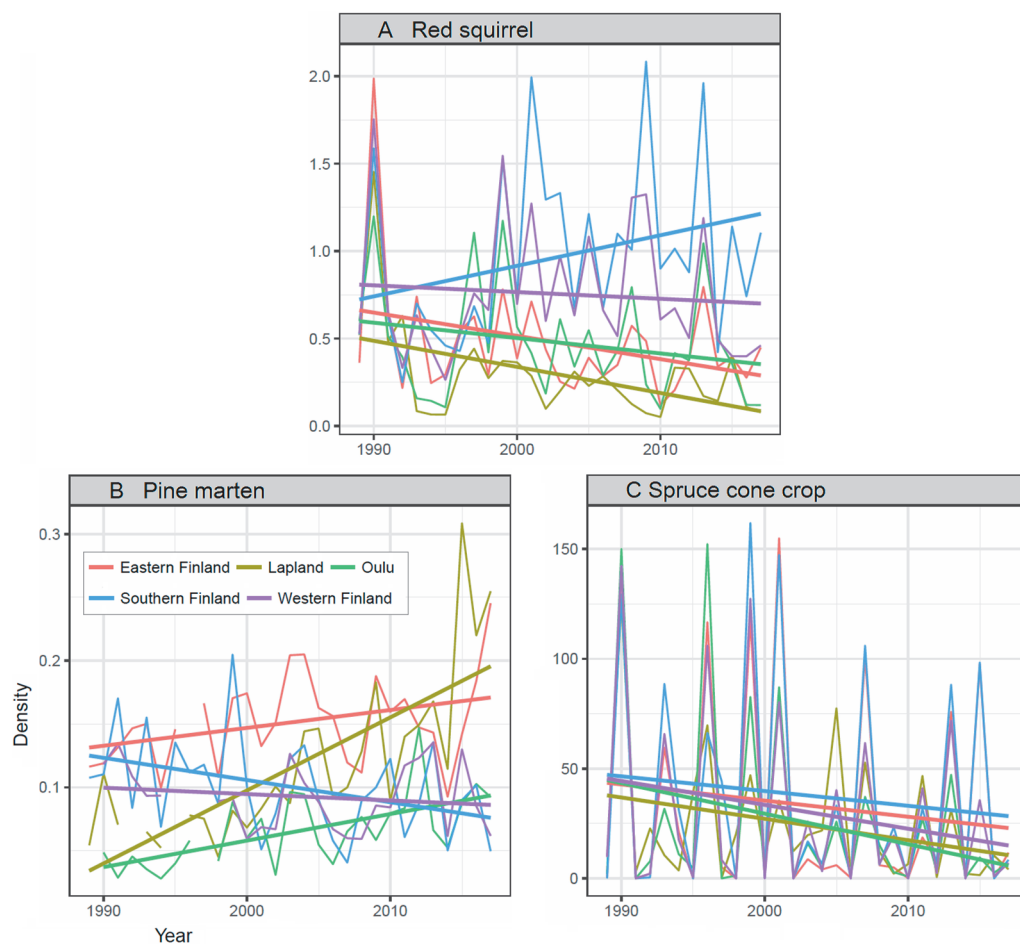


Figure 3. Dynamics of the red squirrel and its food and predators in Finland 1989–2017. Densities of A) the red squirrel, B) the pine marten, and C) modelled level of the spruce cone crop at snow-track census sites in different provinces of Finland. Note that the cone crop in C is previous year's cone crop. Y-axis units in A and B are tracks per 1 km and in C cones per tree. Color legend in B applies to all panels A–C.

The difference in track density between mosaic-like areas and continuous forests also suggests that the dynamics may differ between these landscape types, and is consistent with the results that the red squirrel declined in other parts of Finland while increasing in the southernmost areas. The red squirrel was suggested to have declined in Finland already during the latter half of the 20th century by Selonen et al. (2010), and the analysis of large-scale snow-track data from both Finland and Russia in Chapter IV revealed a declining trend, too. It seems that the red squirrel has been declining in Finnish forests for a long time, and that this decline is still continuing. Snow-track censuses in 2018, not included in the analyses in this thesis, revealed the lowest red squirrel snow-track density during the 30-year census history (Luke 2018c). Possible reasons for the ongoing decline include the global warming, discussed in Chapter IV, and intensive forest management.

While there are still a lot of forests in Finland, old-growth forests are cut down and managed forests are harvested young, and thus, forests are getting younger on average. Mature trees produce more cones, so it could be that the Finnish forests support fewer seed-eaters than before.

All in all, to answer questions stated in The aims of the thesis, the results of Chapter III revealed a remarkable spatial synchrony in red squirrel populations over an estimated range of 650 km, and show that these large-scale fluctuations in the red squirrel density are driven by the climate-driven cone crop, whereas the effect of predators appears weak.

3.4 Population growth rate of the red squirrel under climate change

In Chapter IV, I analysed 17 years of snow-track data from forests in Finland and Russia to calculate regional population growth rates and to study how simultaneous changes in factors potentially important for the red squirrel, especially the ongoing global warming, have affected the long-term population trend. Alarmingly, the results suggest a negative population growth rate in 1996–2012 in 83 % of the 149 regions over a vast area in Finland and north-western Russia (Fig. 4A). The estimated mean population growth rate over all years and all regions was -0.07 , or a 7 % decline per year. However, there is uncertainty in the population growth rate for any individual region, and the high fluctuations characteristic to red squirrel populations complicate the estimation of a long term trend. Also, it has to be noted that although the time series is reasonably long, 17 years, it remains possible that the declining trend is due to transient dynamics. Most regions with negative growth rates were in the eastern half of the study area, between 40° and 60° E, whereas the steepest declines were found in the northernmost parts. An area in south-western Russia stands out with more regions with increasing than decreasing populations, and also southern Finland has some regions with positive mean growth rates. Outside of these areas, there are few regions where the mean population growth rate was positive over the study period. The mean track density was 3.59 per 10 km of census line, with a greater track density in southern than northern parts of the study area. In line with the results of Chapter III, I also found statistical support for processes larger than the size of individual region affecting population growth rates. It is worth noting that the censuses on which the results are based on were conducted in forests. The results do not tell how populations in more human-altered habitats have changed, but based on the results of the Chapters I and III, it seems that the dynamics of the red squirrel populations near human settlement may differ from those in forests. Analyses of possible explanatory variables revealed that the pine marten had mostly increasing populations (in 74 % of regions) at the same time when the red squirrel declined, but these two simultaneous phenomena are not statistically correlated on regional level (Fig. 4B). In other words, the increase in the pine marten density does not explain the decrease in the red squirrel density. Tree canopy cover loss occurred in 3.7% of area within regions, on average, but was not associated with the red squirrel population growth rate.

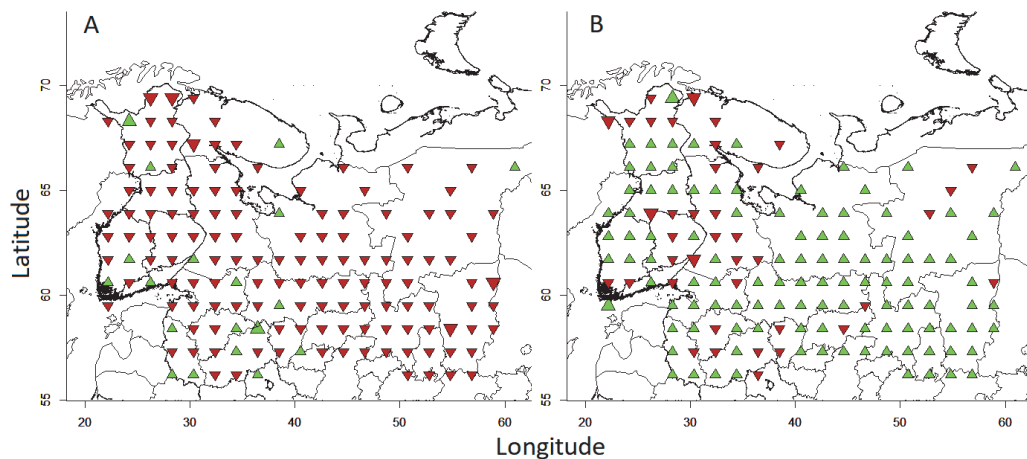


Figure 4. Regional population growth rates (pgr) of A) the red squirrel and B) the pine marten 1996–2012 in Finland and Russia. In both figures, large red triangle pointing down: $pgr \leq -0.2$, small red triangle pointing down: $0 \geq pgr > -0.2$, small green triangle pointing up: $0 < pgr \leq 0.2$, large green triangle pointing up: $pgr > 0.2$.

Analyses of data from 100 weather stations within the study area showed that summers and winters got warmer in the study area (summer $0.087^{\circ}\text{C yr}^{-1}$, winter $0.054^{\circ}\text{C yr}^{-1}$), and precipitation in winter increased (0.14 mm yr^{-1}), which is consistent with the ongoing global warming. Northern and eastern regions warmed more in winter, and the change in winter temperature over the study period was smaller in regions that had warmer mean winter temperatures, i.e. cold areas warmed the most. Of all analysed variables, the regional change in winter temperature was the only one that explained the change in the red squirrel abundance. Red squirrels declined the most in areas where winters warmed the most and where the mean winter temperature was the lowest. However, the increase in the winter temperature only explained 9 % of the variation in the red squirrel population growth rate, so most of the variation remains unexplained. It is also worth noting that as climate is changing, all temporal trends may appear correlated with the ongoing warming. However, I here analysed temporal trends in 149 regions, and found the changes in the winter temperature and the red squirrel track density to be correlated on regional level. For example, there has been a greater change in the summer temperature, used here as a proxy for change in the cone crop (Pukkala et al. 2010) than in the winter temperature, and yet the change in the summer temperature was not statistically associated with the red squirrel population growth rate on regional level.

It remains unclear why the red squirrel would not benefit from a warming climate, as I expected. A number of other temperate and boreal species are shifting their areas of distribution northwards, or increasing in abundance in the northern parts of their range (e.g. Parmesan et al. 1999, Thomas & Lennon 1999, Brommer 2004, Hickling et al. 2006, Parmesan et al. 2006). A warmer climate could mean a more ample cone crop

(Pukkala et al. 2010) and an increased overwinter survival, which is critical especially for subadults (Selonen et al. 2015). However, the limited cone data, which could be evaluated only visually, do not suggest any clear trend, and as discussed above, the increase in summer temperature was not related to population growth rate of the red squirrel. It still seems plausible that some kind of a bottom-up effect could be behind the observed decline, considering the clear effect of cones on red squirrel dynamics in Chapter III and all that is known about the regulation of red squirrel population by fluctuations in resource abundance (e.g. Andren & Lemnell 1992, Wauters et al. 2008, Selonen et al. 2015). Warmer winters could increase the occurrence of insect outbreaks, and consequently decrease the amount of food available for the red squirrel, even when the abundance of cones remains seemingly unchanged. There are many insects which consume seeds within cones, such as lepidopterans *Dioryctria abietella*, *Eupithecia abietaria*, and *E. analoga*, and dipterans *Lasionomma anthracium* and *Plemeninella abietina*. If the overwinter survival of these or other seed-eating insects, or even fungal diseases that weaken trees, is increased, this may cause the kind of relationship between the winter warming and the red squirrel decline as documented here. It is also possible that insects and other decomposers remain active longer during mild winters, and consume fungi cached by red squirrels. This could potentially have some effect because fungi are popular in red squirrels' diet (e.g. Lurz & South 1998; reviewed in Krauze-Gryz & Gryz 2014). Because the changing climate affects so many species, complex interaction cascades are possible, and it is very difficult to say what the mechanism behind declining red squirrel populations is.

It has to be noted that the proxy for habitat loss and deforestation used here, the change in the canopy cover by Hansen et al. (2013), is not ideal for the analysis. Firstly, there is a temporal mismatch; the canopy cover loss data was measured 2000–2014, whereas the red squirrel snow-track data covers years 1996–2012. Admittedly, the loss of tree canopy cover is also a rather coarse measurement and does not give information on habitat quality within the forests that remain. The lack of effect of habitat loss on red squirrel populations here should not be interpreted as an evidence for habitat loss not being important, because habitat loss is the most severe process driving the loss off biodiversity (e.g. Brooks et al. 2002). Rather, the result indicates that the small to moderate deforestation during the study period was not the cause of the decline of the red squirrel on regional level.

In summary, the results of Chapter IV revealed a large-scale decline in the red squirrel abundance index in Finland and Russia during 17 years, 1996–2012. Moreover, I found that the decline of the red squirrel is partially explained by the simultaneous warming of winters. While the exact mechanism behind the decline remains unknown, the results of this study add to the sad evidence of even common and least-concern animals declining worldwide (e.g. Schipper et al. 2008, Ceballos et al. 2017).

4. CONCLUSIONS

In this thesis, I have studied the effects of bottom-up and top-down forces, as well as abiotic factors, on various aspects of red squirrel populations. The studies presented in this thesis describe the different population-dynamic aspects: occupancy patterns in a heterogeneous landscape, sex ratio, year-to-year fluctuation in abundance and long-term trend. Chapters **I-IV** are organized by increasing spatial or temporal scale. Indeed, looking at things on a rather large scale is one of the defining features of this work. Many interesting ecological phenomena, like spatial synchrony and temporal trends, only emerge on a scale larger than an individual population or one field season. The kind of work presented here would not be possible without the contribution of numerous scientists and countless volunteers who have collected data over the years. Therefore, this thesis also serves as a testimony of the importance of long-term and large-scale data collection for gaining insights into the dynamics of wildlife populations.

In Chapter **I**, I studied the effects of habitat type and predators on the nest box occupancy by the red squirrel, and compared the results to those of the flying squirrel in the same area, Kauhava, in central Finland. I found support for habitat-specific predation by the goshawk in a poor-quality habitat. For the flying squirrel, I found a clear detrimental effect of the Ural owl on the nest box occupancy. For both squirrel species the presence of predators, or the predation-risk landscape, seems to determine the nest box occupancy more than the type of the surrounding habitat. Yet, I did not find signs of a trade-off between predator avoidance and settling in a high-quality habitat. In Chapter **II**, I studied how the sex ratio of red squirrel populations varies on a large spatiotemporal scale in Finland, and whether the fluctuating food availability had a role in the variation. The results confirmed the findings of Lampio (1965) that the red squirrel sex ratio varied in Finland in the 1940s, 50s and 60s over large spatial scales. Areas of up to 200 km across had either a female- or a male-biased sex ratio, and the areas of deviating sex ratios were not constant over time, but varied from year to year. However, I did not find any connection between the abundance of spruce cones and the red squirrel sex ratio. A possible mechanism driving such a variation in the sex ratio is the adjustment of offspring sex ratio by females to a local operational sex ratio, as suggested by Ranta et al. (2000). In Chapter **III**, based on analyses of the Finnish snow-track data from 29 years, I found that red squirrel populations fluctuate synchronously over a remarkably large spatial scale. This synchrony seems to be driven by the spruce cone crop, which is similarly synchronized over a scale of hundreds of kilometers. The abundance of the red squirrel was positively correlated with that of the pine marten and modelled goshawk risk index, so predation does not seem to suppress red squirrel populations. Interestingly though, the increasing trend of the red squirrel in Southern Finland coincides with a declining trend in both of the studied predators. This may either reflect a predation release on the red squirrel, or then some environmental change, like urbanization, has opposite effects on the red squirrel and its predators. Outside of Southern Finland, the red squirrel declined, which is the worrying result also in Chapter **I**, from Kauhava, and

in Chapter IV, from forests in the vast area west of the Ural Mountains. The only explanation that I could find for this is the climate change, as warmer winters were correlated with fewer red squirrel snow-tracks on a regional level in Chapter IV. The mechanism of this correlation, as well as other reasons behind the decline, clearly require further studies.

These studies support the view that the population dynamics of the red squirrel are driven more by bottom-up than top-down effects, being more closely linked with the availability of cones than the abundance of predators. The red squirrel is more abundant in spruce forests when there is an ample cone crop (Chapter I) and the density of snow-tracks was higher in those sites and in those years when the cone crop was plentiful (Chapter III). However, food did not explain the variations in the regional sex ratio (Chapter II), and the warming of summers, used as a proxy for the cone crop, was not associated with the long-term declining trend in Chapter IV. It might have been that the trend was less negative or even positive in regions where summers warmed the most and, consequently, the cone crops can be expected to be increasing, but this was not the case. These negative results serve as an important reminder that not everything in the lives of red squirrels is affected by fluctuations in the cone crop. Indeed, I also found some interesting effects of predators. Red squirrels, as well as flying squirrels, were more likely found in nest boxes located in areas of low predation risk by avian predators and red squirrels seemed to avoid or be predated from an especially poor quality habitat, young pine forest, when the predation risk was high (Chapter I). However, on a larger scale, the results of Chapter III showed how the density of the red squirrel is positively correlated with that of its predators. Here, I believe that the shared habitat preferences explain the result. Considering this positive association, it is perhaps not so surprising that the increase in pine marten populations did not explain the decline of the red squirrel in Chapter IV. These results suggests that on a small scale, squirrels avoid or are eaten by predators, but not to such an extent that it would lead to a negative association on population level, where food emerges as the most important determinant of the red squirrel abundance.

We are living in an era when humans alter the Earth with an alarming and increasing intensity. Habitat loss and climate change are the leading courses of defaunation, and many species that are still considered common and of least concern are getting rarer (e.g. Brooks et al. 2002, Walther et al. 2002, Mantyka-Pringle et al. 2011, Dirzo et al. 2014, Paleczny et al. 2015, Ceballos et al. 2017). Therefore, it is important to understand how different species react to different kinds of anthropogenic changes. The red squirrel seems to adapt well to some, but not all, changes caused by humans. Low levels of deforestation, measured as the change in the canopy cover, were not associated with population growth rates (Chapter IV), and the presence of agricultural areas even increased occurrence probability of the red squirrel and the flying squirrel (Chapter I). As I expected, there was, however, a threshold after which squirrels were negatively affected by an increasing area of open farmland, but it was rather high for both species. Both squirrels thus seem to tolerate moderate fragmentation when the matrix consists of

agricultural areas, because forest edges are favorable in this kind of landscape. In Chapter **III**, I observed that the red squirrel snow-track density was higher in the field triangles, situated in mosaic-like areas, than in the wildlife triangles, situated in continuous forests. These results further support the conclusion that moderate levels of habitat fragmentation are tolerated by the red squirrel. The importance of habitat quality, measured as resource availability, was seen in Chapter **I**, where red squirrels favored spruce forests when the cone crop was good. Also urbanization seems to be well tolerated by the red squirrel, and it may even benefit from resources provided by humans (Chapters **I** and **III**). However, arguably the most severe anthropogenic change, the global warming, seems to be detrimental for the red squirrel (Chapter **IV**).

To conclude, the results of this thesis paint a picture of a species that is highly dependent on its fluctuating resources, and while it adapts well to the presence of humans, it has become rarer in forests, much without us noticing. Be the reason the climate change or other anthropogenic factors, such as too intensive forest management, we need to take it as a warning signal, when such a common and well-liked animal is declining.

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