Red squirrels decline in abundance in the boreal forests of Finland and NW Russia

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Abstract

Recent global warming and other anthropogenic changes have caused well-documented range shifts and population declines in many species over a large spatial extent. Most large-scale studies focus on birds, large mammals, and threatened species, whereas large-scale population trends of small to medium-sized mammals and species that are currently of least concern remain poorly studied. Large-scale studies are needed because on a smaller scale, important patterns may be masked by local variation and stochastic processes. Here, we utilized snow track census data from Finland and NW Russia to estimate population growth rates of the Eurasian red squirrel (Sciurus vulgaris L) for a period of 17 years in an area of over $1\,000\,000$ km^2. We also studied the effects of changes in summer and winter temperatures, winter precipitation, predator abundance, and canopy cover on estimated red squirrel population growth rates. Our results suggest that red squirrel populations have declined in most parts of the study area, the only remarkable exception being SW Russia. These results are in concordance with previous studies suggesting that species that are still common and of least concern may be declining. However,our findings are in contrast to the common pattern of northern populations of boreal species increasing due to global warming. The estimated population growth rates are in synchrony over vast areas, suggesting that the underlying reasons also operate on a large scale. We indeed find that the population growth rate was lower in regions where winters warmed faster during the study period, suggesting that changes in the environment (or biotic changes associated with it) are linked with the decline of red squirrels.

Introduction

Rapid climate change is emerging as a major threat to biodiversity in northern latitudes (Ruckstuhl et al. 2008, Gilg et al. 2012). The consequences of global warming are demonstrated in well-documented poleward and altitudinal range shifts of both flora and fauna (e.g. Pauli et al. 1996; Walther et al. 2002; Parmesan 2006). Simultaneous range shifts of several species may result in species turnovers in some areas (Thuiller 2004; Jackson and Sax 2010). Along with climate change, land use and deforestation decrease habitat quality of numerous species to a large spatial extent. As the impacts of global warming and habitat loss accumulate, many argue that we may be in the midst of the sixth mass extinction (Wake and Vredenburg 2008; Ceballos et al. 2015). However, our knowledge of large-scale population trends or effects of climate change are not equally good for all taxa; large-scale studies focus mainly on plants (Walther 2003), birds (e.g. Sanderson et al. 2006; Gregory et al. 2007; Laaksonen and Lehikoinen 2013), and large mammals (e.g. Ceballos and Ehrlich 2002; Post 2005; Bragina et al. 2015). Instead, small to medium-size mammals that are still common and widely distributed remain poorly studied on a large spatial scale.

Climatic conditions are commonly linked to spatial synchrony in population dynamics (Hanski and Woiwod 1993, Paradis et al. 2000). However, large-scale population trends result both from biotic and abiotic processes that occur on a large scale and from processes that present themselves at the population level (Levin 1992; Chave 2013). Large-scale patterns may be masked by local variation and stochastic processes at the population level, highlighting the need for studies over large geographical distances. Such studies can indicate patterns related to underlying processes that can be either inter or intraspecific interactions, environmental factors, or a combination of these (Turchin

1999; Wauters et al. 2008; Wisz et al. 2013). For example, spatial synchrony is an increasingly studied population pattern (Liebhold et al. 2004), where changes (e.g. in abundance) in separate populations of the same or different species occur simultaneously and in same direction. Synchrony can result from many mechanisms, the three most important being environmental forcing, e.g. due to climate (known as the Moran effect, Moran 1953; Royama 1992); trophic interactions (e.g. Byholm et al. 2002; Korpimäki et al. 2005); and dispersal (Ranta et al. 1995). Thus, studying synchrony is essential for understanding the underlying mechanisms, and also improves models on species coexistence and community structure (Bjørnstad et al. 1999; Jones et al. 2016).

The Eurasian red squirrel (*Sciurus vulgaris* L, hereafter red squirrel) is the only native tree squirrel in boreal Eurasia. Although the species is common and widespread, its large-scale population trends remain poorly studied. Red squirrels thrive in many kinds of forest habitats: from boreal coniferous forests to the mixed or deciduous, more temperate forests of Western Europe, and also montane forests (e.g. Wauters et al. 2004; Molinari et al. 2006). In general, red squirrel populations tend to fluctuate around an equilibrium density (Wauters et al. 2004; 2008), but there are some signs that the red squirrel might be declining in parts of its range (Shar et al. 2008; Selonen et al. 2010). Furthermore, the invasive grey squirrel (*Sciurus carolinensis* Gmelin) poses a threat to the red squirrel in Great Britain, Ireland, and Italy. Consequently, red squirrels have declined due to competition and diseases in areas where the two species co-occur (Gurnell and Pepper 1993; Gurnell et al. 2004; Bertolino et al. 2014). Also, complex patterns and shifts from grey squirrels to red squirrels occur locally, but the net change remains from red to grey (Gurnell et al. 2014). Studying trends in countries where the

red squirrel still occurs without the grey squirrel may also prove useful for understanding the red squirrel's population dynamics and coexistence with the invasive species.

Here, our aim is to study population trends of the red squirrel in large spatio-temporal scale, using a 17-year time series of red squirrel snow track data from Finland and Russia. We also aim to assess the impacts of climate change and deforestation on trends in red squirrel abundance, while taking into account predator abundance. Red squirrels live on the northern edge of their range in the northernmost parts of our study area, Finland and North-west Russia. Due to global warming, when several species shift their area of distribution polewards (Parmesan 2006), we expect to see the more northern populations of red squirrels remain stable or increase as a result of milder winters and increased overwinter survival, which is a critical phase especially for subadults (Selonen et al. 2015). We therefore study the effect of change in winter temperature on the regional red squirrel population growth rate. In addition to temperature, precipitation in winter has previously been observed to be related to reproductive success in red squirrels (Selonen et al. 2016), with a potential effect on abundance the following year. In addition, winter precipitation may affect the behaviour or survival of individuals that season. Therefore, the precipitation of both the current and previous winter can affect red squirrel abundance. The summer temperature of the previous year, on the other hand, is one of the most important determinants of the cone crop (Pukkala et al. 2010; see also Bisi et al. 2016 for the effects of climate on conifer seed production). Dynamics of red squirrel populations follow the seed crop of the Norway spruce (*Picea abies* (L.) Karst) and other conifers (Gurnell 1983; Andrén and Lemnell 1992; Kenward et al. 1998; Wauters et al. 2004; Selonen et al. 2015). Squirrel populations are generally

affected by the previous year's cone crop (Pulliainen 1984; Andrén and Lemnell 1992; Selonen et al. 2015, but see Boutin et al. 2006; Wauters et al. 2008), so consequently we use the summer temperature of two years before (Pukkala et al. 2010) to explain the regional population growth rate of red squirrels. Also, decades of intensive forest management in Finland and Russia may have weakened the quality of the habitat for red squirrels (Kurhinen et al. 2006). To account for possible habitat degradation, forest canopy cover data is used as a proxy for habitat quality.

Material and methods

Study area

The study area covers Finland and North-West part of Russia, roughly from 56 to 69 degrees in latitude and from 20 to 60 degrees in longitude, covering about 1 000 000 km^2 (Fig. 1). The main vegetation type is boreal coniferous forest.

Red squirrel snow track data

Throughout this study, we use density of snow tracks as an index of red squirrel abundance. The density of snow tracks correlates strongly with red squirrel numbers (Selonen et al. 2015). The data consist of red squirrel snow tracks from Finland and Russia. In Russia, the monitoring scheme includes a network of sampling locations all over North-West Russia, from close to the Finnish border to west of the Ural mountains. On each census line, snow tracks of all game species are counted yearly one day after snow fall and the length of the census line going through forest, bog and field is reported (Priklonski 1973). We used only data from forests. Forest here refers to all kinds of forested lands and lands in use of forestry, hence also including heavily managed areas and clear-cuts. All this forest land had to be included for accurate

representation of different kinds of forests. The data are summarized on the level of a *rajon*, which is an administrative unit approximately equivalent to a district. The available data covers the years 1996–2012 (see Table 1 for summary of the data). The censuses are governed and the data are provided by The Russian Federal Agency of Game Mammal Monitoring.

The Finnish snow track data originated from wildlife triangle censuses organized by the Finnish Game and Fisheries Research Institute (Rktl) (Lindén et al. 1996), which has recently been merged to the Natural Resources Finland (Luke). The data cover the years 1989–2016, of which years 1996–2012 were used, in order to make Finnish and Russian data sets compatible. The wildlife triangles are established and permanently marked in forests where same routes are censused each year by trained volunteers in January-March. On average 5 triangles are censused each year per 2500 km^2 (Pellikka et al. 2005). The length of each side of the triangle is 4 km, making the total length of census line in each triangle 12 km. The number of snow tracks crossing the census line is expresses as tracks per 10 km of census line per day, meaning days since last snowfall. We used only data that were collected one day after the last snowfall (for both Finnish and Russian track data). During this time, structure of snow does not change so much that it would affect detectability of tracks. Thus, possible changes in environmental conditions during the study period could not affect our data. The raw number of tracks per triangle was calculated from tracks/10km/day and length of the census line. Abundance data of pine marten (*Martes martes* L), used as an index of predation pressure, were collected and processed in the same way.

All spatial locations were expressed in the WGS84 coordinate system. The data were combined and rasterized into boxes of 1.0974 degrees latitude by 2.039 degrees longitude starting from 52.37 degrees northern latitude and 21.175 degrees longitude, which corresponds to grid cell size of roughly 122 km in North-South direction by 102 km in West-East direction (12444 km^2) at latitude 63 N. There were in total 13×20 (latitude $\times$ longitude) grid cells, which we from here on term regions. Note that not all these regions have information on index of red squirrel abundance. Together, this dataset covers a remarkable proportion of the northernmost part of red squirrel's area of distribution.

Climate data

Mean winter and summer temperatures (mean of December, January, and February and mean of May-September, respectively) and cumulative sum of winter precipitation per region were calculated from weather data provided by the Finnish Meteorological Institute (FMI) and All-Russian Research Institute of Hydrometeorological Information - World Data Center (WDC RIHMI). If there was no weather station within a region, the closest one was used. In case of more than one station within a region, only the one closest to the central coordinates of the region was used. The mean winter temperature and sum of winter precipitation for year t were calculated from December in year t-1, and January-February in year t.

Estimation of deforestation and cone production

We used the Global forest cover loss 2000–2014 dataset by Hansen et al. (2013) as a proxy for deforestation. The pixels in the data have a value of either 1 (loss) or 0 (no loss) and a spatial resolution of 1 arc-second per pixel, or approximately 30m (Hansen

et al. 2013). We calculated the mean of canopy cover loss (value between 0 and 1) from all pixels within each region. Canopy cover loss was square-root transformed in order to approximate a Gaussian distribution.

Data on cone crop, based on counts from research forest plots, was available for multiple sites in Finland, but only three sites in Russia. Because of sparseness of data, cone crop was not included in the statistical models, but a trend in cone production or lack of thereof was assessed separately and no trend was observed during our study period (Fig. S1, Table S1). The Finnish cone crop data was published by Pukkala et al. (2010, see also Selonen et al. 2015). The cone data from Pechoro-Ilich reserve, Russia, was collected by T. Tertica and S. Sokolsky and has been published in Annals of nature of Pechoro-Ilich reserve. Because temperature largely determines cone crop (Pukkala et al. 2010) and the actual cone data were sparse, we used temperature in previous summer as a proxy for seed production in further analysis. Actually, this is a procedure currently used in Finland to predict conifer seed production (Pukkala et al. 2010).

Population growth rates
We estimated population growth rates by assuming that the density index of red squirrel snow tracks followed a linear growth on the log scale, which is an appropriate model for stochastic environments (Lande et al. 2003). We assumed data stemmed from two hierarchical processes consisting of the state process (the dynamics) and the observation process. The hierarchical model structure followed standard specifications of state-space models (e.g Kéry and Schaub 2012) and included a component to allow for spatial correlation.

The dynamics for population size N in region i over times t was characterized as

$$\log(N_{i,t+1}) = \log(N_{i,t}) + r_{i,t} + U_i,$$

with

$$r_{i,t} \sim N(\bar{r}_i, \sigma^2_{r,i}),$$

where $r_{i,t}$ is the stochastic population growth rate and $\sigma^2_{r,i}$ is the process variance around the mean population growth $\bar{r}_i$ of region i. Furthermore, we assumed that the dynamics in each region may be affected by common drivers operating on a scale larger than the region considered. The effect of neighbouring regions on the dynamics in focal region i was denoted by U_i, such that the estimated population growth rate of red squirrels when including both regional processes (affecting mean growth rate $\bar{r}_i$), and processes affecting neighbouring regions captured by U was $\bar{r}_i + U_i$. Neighbouring regions of region i were all regions in its queen's neighborhood (also known as the Moore neighborhood), i.e. up to 8 neighboring regions were considered. The U term thus models the potential influence of spatially correlated processes occurring at a spatial scale larger than the region. These spatial correlations were modelled using an intrinsic conditional autoregressive (ICAR) structure (Besag et al. 1991), where

$$U_i | U_j, j \in \partial_i \sim N\left(\bar{U}_i, \frac{\sigma^2_U}{n_i}\right).$$

Here, for each region i which had one or more neighbouring regions (whose identity is contained in the set ∂_i), U_i is normally distributed around $\bar{U}_i$, the mean effect of all region i's neighbouring regions, with a variance σ^2_U/n_i, where n_i is the number of neighbours of region i. The ICAR distribution is internally scaled to be a random effect which is normally distributed around an overall zero mean. For regions without neighbours with data $U_i = 0$. When σ^2_U is substantial, these random effects are spatially

ordered such that the value of U_i is similar in value for regions which are neighbours (see Banerjee et al. (2004) for more details on CAR models). Thus, dynamics will then be spatially autocorrelated as U will create positive or negative changes in population growth rate for neighbouring regions. However, when regions are largely spatially independent, σ_U^2 approaches zero, and thus U_i will be zero, and the dynamics are then largely governed by regional population growth rate r_i only. Hence, a measure of the degree of spatial dependency of neighbouring regions in population growth rate is the ratio between σ_U^2 and $\sigma_{r,i}^2$. The ICAR distribution is a classic approach to modeling spatial autocorrelation especially when a large number of sites are considered.

The observation process was assumed to have normally distributed errors, such that

$$\log(y_{i,t}) \sim N(\log(N_{i,t}), \sigma_{o,i}^2),$$

where $y_{i,t}$ is the observed track density index, and $\sigma_{o,i}^2$ is the variance in the observation error. The model was implemented in WinBUGS 1.4 (Lunn et al. 2000), which allows for the ICAR structure. For a prior probability distribution for initial population size, we used a normal distribution with mean equal to the track density in each region i in the first year and with standard deviation of 10. For mean growth rate, we used a uniform (flat) prior. For priors of the *SD* of both the region-specific state and observation processes, we used uniform distribution between 0 and 1. The prior for the ICAR distribution was chosen following WinBUGS instructions (Lunn et al. 2000) with the precision based on a gamma distribution with shape of 0.5 and a rate of 0.0005. Running the model with different priors produced qualitatively the same results.

Assessment of trends in climatic variables

Our objective was to test whether regional population growth rates were related to temporal changes in temperature and precipitation. We calculated a trend for changes in climatic variables for each weather station in the study area with data available for at least part of the study period based on a random regression (Henderson 1982) of temperature or precipitation on year, where an intercept and slope for each station was calculated. Thus, we assumed that the temperature *T* for station *s* in year *t* was

$T_{st} = \square + \square \; year_t + i_s + b_s \; year_t \,,$

where $\square$ is the overall, fixed-effect intercept (i.e. mean temperature), and $\square$ the overall, fixed-effect slope, *year* is a continuous variable of the study years rescaled to have a mean of zero i.e. year varied from −8 to +8). The parameters i_s and b_s are random deviations from the fixed-effect intercept and slope respectively. These parameters thus model the station-specific mean temperature (at *year* = 0) and the annual change in temperature during the study period. These parameters were assumed to stem from a bivariate normal distribution with means of zero and a (co)variance matrix. Thus, random-regression models both the change experienced over the entire region (the fixed effect slope) and allows estimation of specific annual trends for each station while acknowledging these trends are derived from a single distributional process and hence not fully independent (Pinheiro and Bates 2006). This model was implemented in WinBUGS (Lunn et al. 2000). We used the station-specific slope calculated as the mean of the sum of posteriors of $\square$ and b_s as an estimate of the annual change in temperature for each weather station. Slopes for precipitation were calculated in the same way.

Relating changes in the environmental variables to population changes

We assessed whether changes in the environmental variables and pine marten abundance affected region-specific long-term changes in the abundance index of red

squirrels, including the spatial autocorrelation between neighbouring regions (calculated as $\bar{r}_i + U_i$), with a linear multivariate model implemented in R (R Core Team 2016). Interactions between the explanatory variables were not significant and were dropped from the final model. Because winter precipitation in 1995–2011 and in 1996–2012, representing different mechanisms how precipitation can affect red squirrel abundance (see introduction), are highly correlated, they were used in separate otherwise identical models. Results were essentially identical, and we hereafter consider current year's precipitation (1996–2012) when referring to winter precipitation.

Results

There were 149 regions with enough data (12 or more years out of the 17). The mean track density was 3.59 per 10 km of census line (range 0.45–9.49, Fig. 1a,b). The time series are illustrated in Figure 2. The overall track density during study period was highest in South-West parts of Finland and Russia and decreased towards northern and eastern edges of the study area (Fig. 1a; the effect of Y and X coordinates on track density: multiple linear regression: $F_{2, 146} = 50.51$, $P < 0.001$, $R^2 = 0.40$). Because the northernmost part of the study area is at the same time the northern edge of red squirrel's area of distribution, density was expected to decrease to that direction.

Population growth rate was negative in 83.2 % of regions, and the mean growth rate over all years in all regions was –0.07 (range –0.58, +0.50, Fig. 1c). Because of the relatively short time series, the uncertainty in population growth rate for any individual region was, however, substantial as indicated, for example, by the upper 90 % posterior probability being below zero in only 1.3 % of the regions. The mean proportion of U

(the measure of spatial correlation) from total process variance, i.e. the mean ratio between σ_U^2 and the sum of σ_U^2 and $\sigma_{r,i}^2$, was 0.17, which means that also spatial processes larger than region size affected population growth rates, in addition to local processes. The most negative growth rates were found in Finnish Lapland, and overall the results show a uniform decline, only remarkable exception being a cluster of cells with positive growth rates in South-West Russia (Fig. 1c; Fig. S2).

Association of the estimated population growth rate to environmental variables
Pine marten abundance index did not show a similar decline as red squirrels' (Fig. 1d) with 74% (110/149) of regions showing increases in pine marten abundance index with an average population growth rate of 0.013 [95% CRI –0.19, 0.12] across all regions. Tree canopy loss occurred on average in 3.7 % of pixels within a region (range 2.4–10.3 %). There were 100 weather stations in the study area with sufficient data to calculate annual changes in weather variables. Overall, trends were consistent with climate changing during the study period: summers and winters got warmer in the study area (summer: fixed effect slope b = 0.087 C/year, 95% CRI [0.080, 0.095]; winter: b = 0.054C/year [0.023, 0.085]), and precipitation in winter increased (b = 0.14 mm/year [–0.21, 0.47].

A multivariate model indicated that the regional change in winter temperature was the only variable associated with the regional change in red squirrel abundance index (Table 2; Figs. 3, 4, S2, S3.). Northern and eastern regions warmed more in winter (Fig. S3). The change in winter temperature over the study period was lower in regions that had warmer mean winter temperatures (random regression: *r* intercept-slope = –0.63 [–0.98, 0.23] and changes in the other climatic variables were similarly correlated to their mean

value. Because of this collinearity, we can only consider the effect of mean climatic variables as an alternative model, which showed that red squirrel decline was strongest in regions with low mean winter temperature (Table S1), thus strengthening the notion that (changes in) winter temperature are associated with changes in the abundance index of red squirrels.

Discussion

Our findings based on a 17-year time series show that red squirrel populations have been declining in vast parts of Finland and North-West Russia and that estimated population growth rates show spatial synchrony over large scale. We expected that density indices in the northernmost populations would show a higher growth rate than regions in the southern part of the area of distribution, because global warming is hypothesized to make northern areas more suitable for temperate mammals. However, we find that most of the (few) regions with increasing population density indices are in South-West Russia, whereas most regions with strongest decline are in the northern parts of the study area. We consider both top-down and bottom-up regulatory factors, and find that the regional (change in) winter temperature is associated with the rate of the regional decline in the abundance index of red squirrels' populations. Regions where the average winter temperature is low and the rate of winter warming is faster show stronger declines. These findings provide further evidence that – counter to our expectation – climate change is not beneficial for the red squirrel.

Many of the species that have been observed to increase in density in northern parts of their range or to shift their range northwards due to global warming have been very mobile species like birds (e.g. Thomas and Lennon 1999; Brommer 2004; Hickling et

al. 2006) and butterflies (e.g. Parmesan et al. 1999 ; Hickling et al. 2006; Pöyry et al. 2009). There are only few studies showing that also less mobile species, like terrestrial mammals, expand their ranges (Davis and Callahan 1992; Hickling et al. 2006; Moritz et al. 2008). While range expansion occurs on average, these studies also find that not all of the species in the assemblage considered actually showed range expansions. This heterogeneity in response has been explained by differences across species in which aspect of the climate they are sensitive to, as well as differential responses to these changes (Tingley et al. 2012). Indeed, by modeling the ability of mammals to keep pace with projected climatic changes, Schloss et al (2012) predicted that on average 9.2 % of terrestrial mammals will not be able to track climate change during the coming century. Our results provide a detailed and large-scale documentation of a species not increasing in density, let alone extending its range towards more northern areas. The declining trend in existing red squirrel populations is not because the species has limited mobility to respond to climatic changes, but appears to be caused by factors which are spatially correlated. Regional conditions, likely related to (changes in) winter temperature, are becoming unfavorable for red squirrels.

Warming shows temporal asymmetry, some seasons have warmed more than others, and, depending on time scale, winters in some parts have even cooled (Cohen et al. 2012). Our analysis of meteorological data shows, however, that within our study area and 17-year study period, winters did warm with an overall average of 0.5C/decade. Given that red squirrels show an overall decline in population sizes during the study period, it is clear that any variable which shows a trend over this period will appear to be associated to the numerical decline of red squirrels. However, we here consider changes in the index of abundance of red squirrels in 149 regions over a large spatial

scale, and find that these changes are associated with climatic conditions during winter in these regions. There are clear differences between the regions; some are on average colder and have warmed more compared to other ones and this pattern in winter climate is associated with the change in red squirrel abundances. While such an association may arise because of a variety of reasons, there is no *a priori* expectation that inter-regional variation would covary with climate during this specific period without a causal reason on some level. Indeed, we also find that, for example, summers have gotten warmer on average, without this warming being associated to population growth rate on the regional level. Still, it remains unclear why red squirrel populations would decline any faster in regions where winter weather is cold and has warmed more rapidly. The abundance indices we use are based on snow tracks counted in winter, which raises the possibility that warmer winters affect these counts because of some methodological reason. The counts are standardized to be carried out after fresh snow fall, and are carried out during a period of winter conditions. Thus, there is no direct connection between the warming trend and the conditions the survey data are collected. One possibility would be that the propensity to detect red squirrel snow tracks would decrease when winters get warmer, but squirrels are likely to move more, and not less, during warmer periods (Lampio 1967; Pulliainen 1973; Doebel and McGinnes 1974). Based on our earlier analysis snow-track numbers are positively correlated with squirrel numbers in nature (Selonen et al. 2015). We therefore believe that the decrease in snow tracks signals a true decline in population size of red squirrels. Warmer winters are, of course, beneficial to many species and one possibility therefore is that winter warming increases the competition and/or predation and/or disease risks for red squirrels or for their food (seeds). Lastly, we note that the association between regional winter warming

and population growth rate, while significant, is very modest (r approximately –0.3; thus winter warming explains about $0.3^2 = 9\%$ in variation of growth rate).

Although our study period is reasonably long (17 years), it remains possible that the observed decline in our index of abundance during this study period is due to transient dynamics. For example, red squirrels are dependent on conifer seeds and their population dynamics are heavily affected by the availability of this food resource (e.g. Rajala and Lampio 1963; Gurnell 1983; Andrén and Lemnell 1992). However, the few cone data that we have from Russia and the comprehensive Finnish cone data show no temporal trend (Fig. S1, Table S2) and in the current model we controlled for possible variation in mast conditions by taking into account weather conditions that account for the tree mast (Pukkala et al. 2010; see methods). Thus, we conclude that cone crop, although generally the backbone of squirrel ecology, is not associated with changes in the red squirrel population abundance index which we document here. Clearly, the only way to get a handle on the likelihood and role of transient dynamics of red squirrels is to collect long-term monitoring data. Thus, our study demonstrates the importance of coherent long-term data collection over large scales for gaining insights in the dynamics of wildlife populations.

Most previous studies on red squirrel population trends have taken place in countries where the invasive grey squirrel competes with native red squirrel. These studies have shown red squirrel to decline and grey squirrel to increase in Great Britain, Ireland and Italy (Gurnell and Pepper 1993; O'Teangana et al. 2000; Gurnell et al. 2004; Bertolino et al. 2014). Wauters et al. (2004) studied red squirrel populations using capture-mark-recapture methods in Belgium, where grey squirrels do not occur, for nearly 10 years,

and found the populations to fluctuate around an equilibrium density, with no trend. Previous indirect studies in Finland (Selonen et al. 2010), in contrast, suggested that red squirrels have been declining. Our findings support this and may further suggest that there are even more threats than just a competitive species for red squirrels in Europe. The nearly uniform decline across regions that we find is in concordance with reports suggesting that many still common and least concern mammal species are currently declining (Schipper et al. 2008). We further find clear evidence that processes on a scale larger than the individual regions are underlying these declines; most regions show a decline in population density index. Statistically, large-scale processes manifest themselves as spatial correlations in population dynamics between neighboring regions. Hence, our findings strongly point at large-scale processes such as climate change being involved in the decline of red squirrels. Out of a number of top-down and bottom-up regulatory factors, we find that (changes in) winter temperature is negatively associated with the observed change in red squirrel abundance index but more detailed studies are needed to explore the causal basis of this association.

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Figure 1: a) Red squirrel snow tracks densities (tracks per 10 km of census line) over the study period 1996–2012 in Finland and northwestern Russia. White: 0 < density <=2, light green: 2 < density <=4, smaller dark green: 4 < density <=6, larger darker green: 6 < density <=8, black: density > 8. b) Histogram of track densities from the same data. c) Population growth rates (pgr) of red squirrels, including the spatial autocorrelation of neighbours, in Finland and northwestern Russia 1996–2012. Large red triangle pointing down: pgr <= -0.2, small red triangle pointing down: 0 >= pgr >- 0.2, small green triangle pointing up: 0 < pgr <=0.2, large green triangle pointing up: pgr > 0.2. d) Population growth rates (pgr) of pine martens from the same study period. Large red triangle pointing down: pgr <= -0.2, small red triangle pointing down: 0 >= pgr >-0.2, small green triangle pointing up: 0 < pgr <=0.2, large green triangle pointing up: pgr > 0.2.
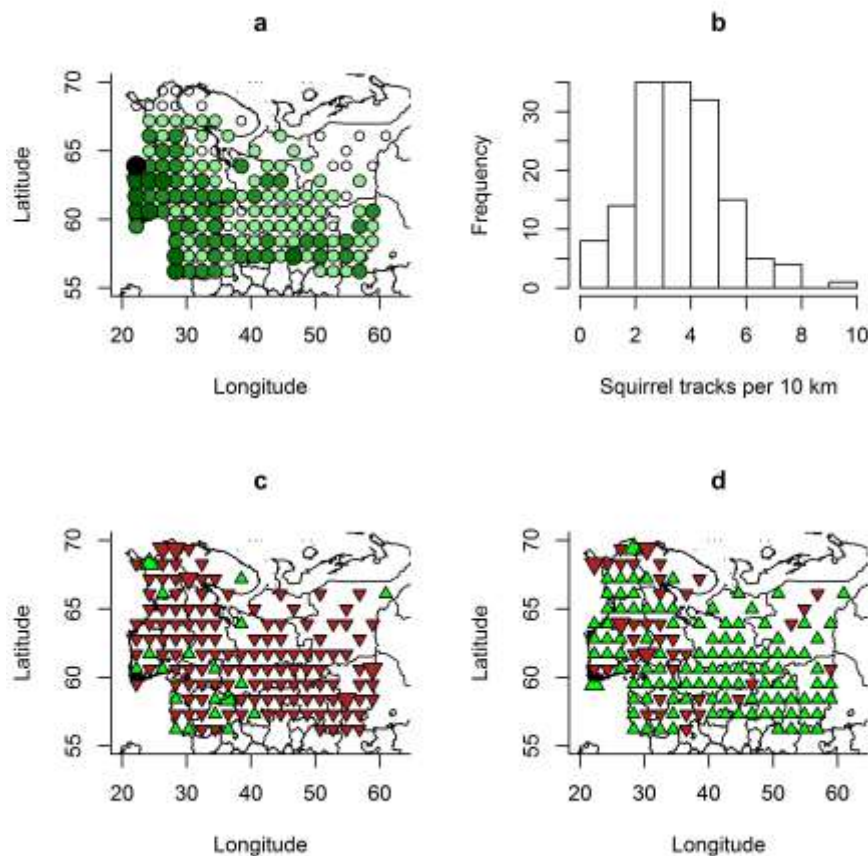
Figure 2: The time series. The Y-axis shows the logarithm of mean track index per year. Open dots with solid line: Finnish data. Filled dots with dashed line: Russian data. For analyses we used data from the time period for which we have data from both countries (1996–2012) and the data on Finnish track counts are hence only plotted here for the sake of comparison. Data since year 2014 are based on means per game management area instead of triangle –level data in earlier years.
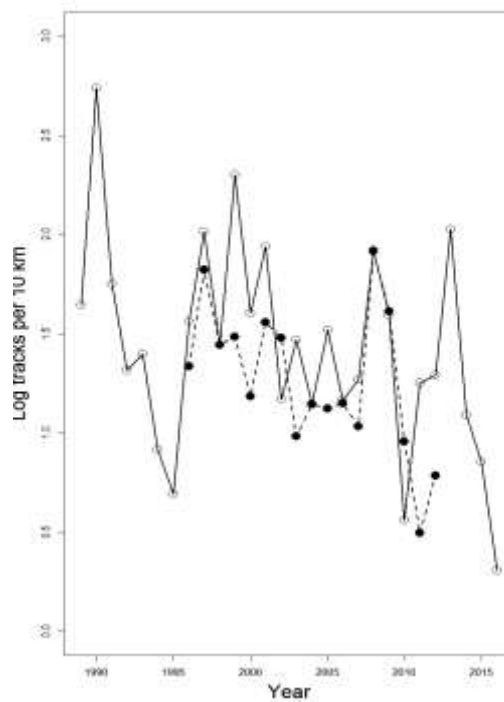
Figure 3: Plots of regional population growth rate for all 149 regions considered including the spatial autocorrelation of neighbours versus climatic variables. (a) mean change in summer (May-Sep) temperature in °C/year, (b) mean change in winter (Dec-Feb) temperature in °C/year, and (c) mean change in winter precipitation (ml/yr). The dashed line indicates zero population growth. The black line in (b) is the linear regression line drawn as illustration of the significantly negative correlation between population growth rate and winter warming, but none of the other environmental variables correlated significantly with population growth rate (see text).
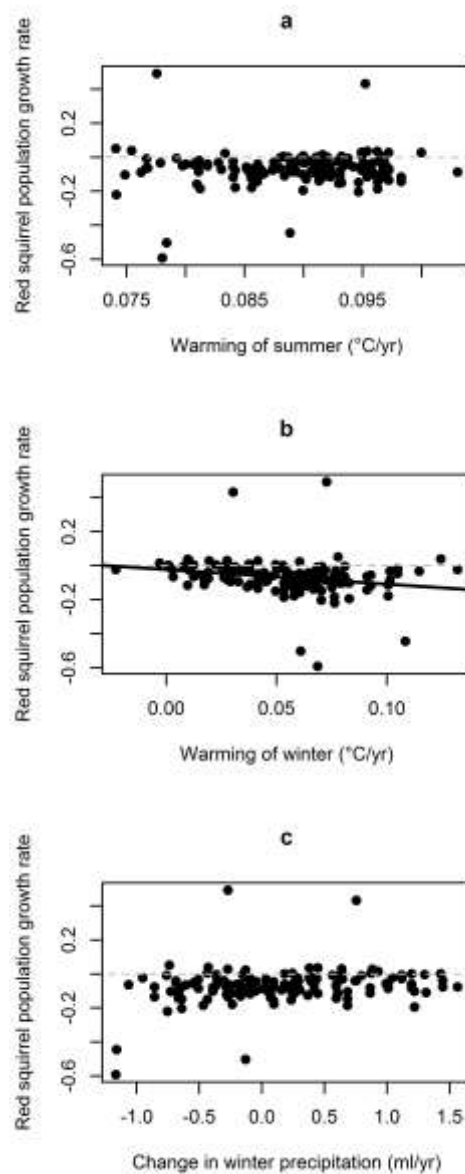
Figure 4: Regional population growth rate for all 149 regions considered including the spatial autocorrelation of neighbours versus changes in biotic factors. (a) proportional loss of canopy cover (sqrt) and (b) change in pine marten population growth rate, also including the spatial autocorrelation of neighbours. Dashed grey lines indicate zero population growth.
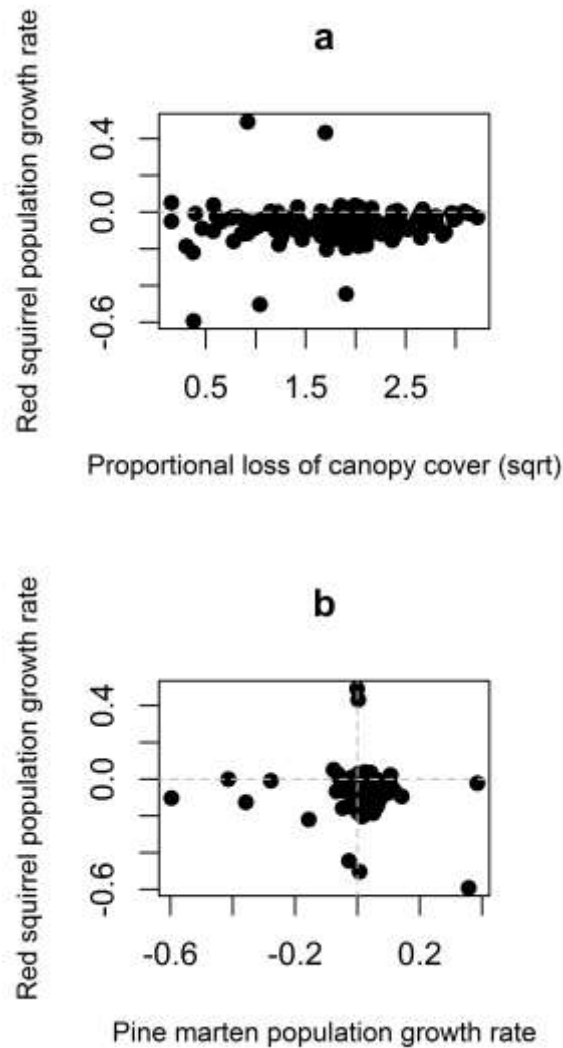
TABLE LEGENDS

Table 1: Summary of the data. N (nuber of individual census lines for Finland and number of districts (*rajons*) with summarized census data for Russia), length of census line in kilometers (rounded to nearest km), and mean (±SE) number of tracks per 10 km of census line in forest per year in Finland and Russia.

		Finland			Russia	
Year	N	Total length of census line, km	Tracks per 10 km (mean ± SE)	N	Total length of census line, km	Tracks per 10 km (mean ± SE)
1996	569	6830	4.78 (±0.3)	126	19394	3.80 (±0.2)
1997	609	7312	7.50 (±0.6)	323	68337	6.19 (±0.2)
1998	563	6765	4.24 (±0.3)	313	75839	4.23 (±0.2)
1999	454	5448	9.98 (±0.9)	322	82830	4.41 (±0.3)
2000	524	6295	4.97 (±0.4)	299	75380	3.27 (±0.1)
2001	474	5693	6.97 (±0.6)	322	83834	4.75 (±0.2)
2002	457	5485	3.23 (±0.2)	318	78192	4.38 (±0.2)
2003	405	4860	4.35 (±0.4)	320	84135	2.68(±0.1)
2004	495	5940	3.15 (±0.2)	313	73653	3.14 (±0.1)
2005	412	4937	4.57 (±0.4)	321	82313	3.07 (±0.1)
2006	385	4620	3.21 (±0.2)	322	81791	3.16 (±0.1)
2007	324	3888	3.56 (±0.3)	340	90041	2.81 (±0.1)
2008	344	4129	6.81 (±0.6)	320	77115	6.80 (±0.3)
2009	319	3823	4.94 (±0.5)	303	79857	5.02 (±0.2)
2010	207	2485	1.75 (±0.3)	306	82156	2.61 (±0.1)
2011	283	3387	3.49 (±0.4)	304	82445	1.64 (±0.1)
2012	272	3387	3.64 (±0.4)	264	63861	2.19 (±0.1)
Mean	417	5725	5.10	302	75363	3.77

Table 2: Linear model of the change in red squirrel abundance index during 17 years (1996 – 2012) in a region as a function of the change in several variables relating to a higher trophic level (population growth rate pgr of pine martens), as well as the landscape (proportional forest loss) and climate (summer and winter temperature and winter precipitation). The significant variable is indicated in bold.

Variable	Effect s.e.	$F_{1,143}$	P
Intercept	0.095 0.14		
pgr pine marten	–0.14 0.092	2.2	0.14
prop. loss forest	–0.0017 0.0038	1.1	0.29
change in summer temperature	–0.91 1.4	0.6	0.43
change in winter temperature	**–1.5 0.81**	**7.0**	**0.009**
change in winter rain	0.030 0.017	3.1	0.08