UiT

THE ARCTIC
UNIVERSITY
OF NORWAY

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Estimating population trends of a riparian bird community in low-Arctic tundra

—

Clémence Koren
BIO-3950 Master thesis in Biology
February 2018

UNIVERSITY OF TROMSØ

Master's thesis

—

ESTIMATING POPULATION TRENDS OF A RIPARIAN BIRD COMMUNITY IN LOW-ARCTIC TUNDRA.

—

Clémence Koren

Supervised by:
R. A. Ims
J.-A. Henden
N. G. Yoccoz

15th February 2018

Abstract

In the Northern Norway tundra, willow thicket along river valleys create a more productive environment than the surrounding open tundra and host a rich community of bird species by providing food, shelter from predators and nesting site. The state of Arctic ecosystem is expected to undergo long-term changes due to opposite effects of climate change and herbivory pressure. It is also the background of a large natural temporal variability in small rodent population cycles and date of onset of spring. This study aims at evaluating the status of the riparian bird community and at investigating the effects of temporal variation in rodent abundance and onset of spring on the growth rate of bird species.

Bird abundance was recorded in the Varanger Peninsula, during seven years over the period 2005-2016, using a spatially and temporally repeated point count sampling method. A hierarchical model (the generalised N-mixture model of Dail and Madsen) is used to estimate the abundance and growth rate while taking into account the detection probability of the recorded species. The effects of spatial and temporal variables on abundance, detection probability and growth rate are estimated through the inclusion of environmental covariates in the model.

Two species, the rough-legged buzzard and the willow grouse had a negative population trend, to the point of reaching local extinction. No other species exhibited discernible population trends, despite the general loss of total abundance, species richness and occupancy of the bird community. No clear long-term change in the onset of spring or the rodent abundance was found, but a few species were found to benefit from an earlier onset of spring or from higher rodent densities.

This indicates that the studied bird community is generally getting poorer. However, if long-term environmental changes happen in accordance to climatic predictions, spring events will occur earlier, rodent cycles might dampen and the shrub thicket habitat could gain in areal extent. Thus, species will probably show differential responses to these environmental changes. Species able to adapt their phenology to future temporal changes, species that already benefit from earlier onset of spring and species with a low level of habitat or diet specialisation will be expected to perform better than other less adaptable species.

This study provides more insight in the status of the bird community associated with the low-Arctic riparian willow thickets by revealing the virtual local extinction of two species in the studied region and the general impoverishment of the community. Longer-term monitoring will be needed to observe clear trends in the population of other species and to determine the effects of environmental changes on the bird species.

1

Acknowledgements

I would like to thank my supervisors for their support and for giving me the opportunity to work on such an interesting project, T. Tveraa for taking the time to calculate the onset of spring data, G. Vie for a very inspiring fieldwork experience, and all the members of the COAT Team involved in the collection of bird point count, rodent abundance and thicket structure data.

I am also very grateful to my parents for supporting my choices despite the distance and the rarity of our reunions, to Lucie and Camille for their friendship over the years, and to Amund and Alicia for meeting them when I needed it the most.

Table of Contents

List of Figures

List of Tables

1 Introduction

1.1 The importance of population monitoring

The past decades have been the stage to changes in the ecosystems and biodiversity. Since 1970, most of the sources of pressure on biodiversity (pollution, invasive alien species, over-exploitation, climate change impacts) have been increasing [4]. Climate tends to become less predictable with an increased weather variability and a higher frequency of extreme events [25].

Indicators of the state of biodiversity (species population trends and extinction risk, community composition, habitat condition) have showed a general loss of biodiversity worldwide [4].

Negative trends in abundance have been observed for vertebrates and habitat-specialist birds, along with the reduction and deterioration of habitats such as forests, mangroves or coral reefs [5].

Species of vertebrates, amphibians, insects and plants have also shown changes such as northward and upward shift in range and earlier onset of spring events (flowering and budding, larvae hatching, migration and/or breeding timing) that are consistent with the predictions of climate change impacts [28].

In such a changing environment, monitoring of species is required in order to keep track of biodiversity responses to environmental changes and to understand how dynamic ecosystems and food-webs react and adapt.

1.2 Climate change and temporal variability in the Arctic

The polar region seem to be more severely affected by climate change than other regions [19]. Because minimum temperatures increase twice as fast as maximum temperatures, the global temperatures are rising, leading to longer periods above freezing levels, and a reduction of the snow cover and sea ice extent [43]. Consequences of such changes are already observable and are expected to increase in the future, with shifts in the geographical ranges of northern species towards higher latitudes and altitudes, range expansion of more warm-adapted species and more frequent outbreaks of pest species, shrub encroachment of open tundra, and phenological changes [27, 25, 17].

Arctic ecosystems are also characterised by a high seasonality. Due to their high latitude, they experience periods of constant sunlight or absence of sun. The climate is colder and harsher than in most other biomes on Earth. The growing season is condensed in the few sunlit months or weeks

in summer and the ecosystems are generally less productive than more temperate systems. Many species are only active throughout these few summer months, due to dormancy (plants and insects) or migration (most birds).

Onset of spring seems to be advancing, and this can be critical for a system where the growing season is so narrow. Many species are thus adapted to a specific timing of events (e.g., migratory birds and their date of arrival on the Arctic breeding ground, or their laying date) and might experience mismatches and difficulties if the environment timing changes [27]. Other species are constrained by this narrow growing season and might benefit from an earlier spring, by having a longer period of food availability, by being able to breed twice consecutively, or by being able to colonise higher latitude than their usual range [41].

Birds' migratory behaviour has been shown to be of importance in this context. By spending a part of their yearly cycle away from their Arctic breeding ground, migratory birds can experience difficulties tracking the abundance of food or the habitat condition [25]. Climate change can lead to changes in the phenology of insects and vegetation, potentially leading to mismatches between a migratory bird and its source of food, because the phenology of the bird often depends on different cues and triggers than the phenology of their food source. Long-distance migrants often show different intensity of population decreases than short-distance migrants and resident species, but it is unclear which strategy is the most vulnerable [35, 22]. Diet can also be hypothesised to be of importance, especially if the case of phenological mismatches arises [25]. The most successful species are expected to be the species with the broadest diet, capable to switch to alternative prey, and species that are able to adapt their phenology to a changing environment. It is unclear yet what the results of climate change are on migratory bird species as a whole and it is likely to depend on a combination of several factors (e.g., inter-specific interactions such as predation, intrinsic specific ability to adapt phenologically, additional environmental conditions and disturbances).

Another characteristic of most Arctic terrestrial regions is the presence of a guild of small rodents considered as key species in these ecosystems. Indeed, they are both a favoured prey to many mammalian and avian predators, and an herbivore having a substantial effect on the vegetation, placing them at the core of most Arctic food webs. They also typically exhibit large year-to-year fluctuations in population abundance, following regular cycles that are synchronous among species and over large regions. These cycles are shown to be the driver of population cycles in other species through direct trophic link or indirect effects such as facilitation or competition [14, 15]. In the recent decades however, these cycles have been dampening and getting more irregular in many regions, possibly due to warmer winter climate [11]. The

consequences of the loss of these cycles on the whole ecosystem are heavily studied, but are still unclear for the most part.

Such within- and between-year variability in environmental conditions makes the Arctic tundra a highly dynamic system that calls for long-term monitoring in order to differentiate between the natural temporal variability inherent to the ecosystem and the potential presence of long-term trends in population abundance or environmental characteristics.

The COAT project (Climate-Ecological Observatory for Arctic Tundra), is a large-scale, long-term, food-web based, adaptive monitoring program aiming at tracking changes and identifying trends in Arctic systems [17]. One of the study region of COAT is the Varanger peninsula in Northern Norway. Its location at the transition between tundra and boreal forest makes it a critical region to study the impacts of climate change on the state of the vegetation and the status of animal species [17].

1.3   The Varanger Peninsula ecosystem

The Varanger peninsula presents a typical low-Arctic tundra ecosystem, with open areas of dwarf shrubs, and more productive areas along river valleys, with lush meadows and thickets of tall willow shrubs [39, 17]. These thickets create productive hotspots of biodiversity by providing food, shelter from predator and breeding habitat for many bird species.

The height and areal extent of these thickets positively affect the bird species abundance, occupancy, and the community richness [12], and even species typically found in open tundra habitat benefit from the presence of an intermediate level of thickets [16]. Predictions for the future of the Arctic tundra under climate change conditions indicate an increase in shrub extent leading to an enrichment of the bird community. However, if herbivory from reindeers and rodents leads to a decreased shrub cover, the bird community is likely to loose species and species-specific abundances [12].

However, given the high cyclic nature and temporal variability of this system, it is likely that the temporal variation will have an effect on the bird community dynamic. High variability of environmental variables and their effect on bird species can also give an indication of the future changes that can be expected in the community, if environmental changes lead to durable trends in these variables. Most of the variability observed in the Arctic tundra can be attributed to the date of spring (directly impacting the phenology of insects and plants) and rodent cyclic dynamic (directly impacting the vegetation and the guild of predators). It is yet unclear how the natural temporal variation underwent by these ecosystem affects the bird

community and what the effects of modified dynamics in these environmental conditions might be.

1.4   Aims and predictions

This study aims to (i) investigate the changes in abundance of this low-Arctic bird community and the possible presence of temporal trends and (ii) evaluate the effect of environmental temporal changes in rodent abundance and onset of spring on the bird species growth rate.

According to previous studies, long-distance migrants are expected to have a globally lower growth rate than short-distance migrants and resident species, and to be more sensitive to the onset of spring than species wintering closer to the Arctic breeding grounds. Species associated with tall shrub are expected to perform generally better than strictly open-tundra species in a context of Arctic climate change and range expansion of more boreal species. Rodent population cycles are known to affect a large part of the ecosystem, but it is unclear how the riparian bird community is affected by this temporal variability. Species with a broader diet are predicted to perform better than more specialised species if phenological mismatches are occurring.

2 Material & Methods

2.1 Study Area

Geography and vegetation

The study took place in the Varanger Peninsula (Northern Norway), over three regions located at similar latitudes (between 70°15'N and 70°25'N) : Ifjord (IF), Komag (KO) and Vestre Jakobselv (VJ) (Figure 1). In each region, one or two river valleys with sections of tall shrub thickets were selected. Along these valleys, we determined sampling points (8 to 9 per region - 25 in total) at locations presenting varied levels of shrub areal extent and fragmentation.

According to the Circumpolar Arctic Vegetation Map classification, this area belongs to the southernmost edge of the bioclimatic sub-zone E "Arctic shrub sub-zone". This sub-zone is characterised by a thick moss layer (up to 10 cm), a dwarf-shrub or herbaceous layer (up to 50 cm) and sometimes a low-shrub layer (up to 80 cm) [42, 39]. However, due to micro-topography and its impact on temperature gradient, water drainage and snow accumulation patterns, river valleys are often more productive than the surrounding flat open tundra and are thus able to accommodate lush meadows and tall shrubs (mainly willow *Salix* and sometimes alder *Alnus*) up to 2 meters [17].

Willow thicket structure

The willow thicket structure of each sampling point is described by three variables measured in 2006 in Henden's study [12]. *Willow area* is determined from aerial photographs (pixel resolution = 20 cm) as the percentage of ground covered by willow in a 200×200 meters quadrat centred on each sampling point. To assess the height and density of the thicket, a 15-meter interval that includes the sampling point was set along the border between the thicket and the meadow. At four points along this interval, a stick was placed vertically 1 m inside the thicket. At each stick, the tallest branch in a 20-centimetre radius circle is measured, and the number of hits with leaves and secondary stems and branches is recorded, following a modified point-frequency method. The *willow height* and *willow density* variables are calculated as the average value over each of the four respective measurements.

No new measurements have been done since 2006, but no discernible changes have been visually observed during the study period. These variables show a high overlap over the three regions [12] and they are only slightly correlated, with Pearson's product-moment correlations $-0.13 < r < 0.22$.
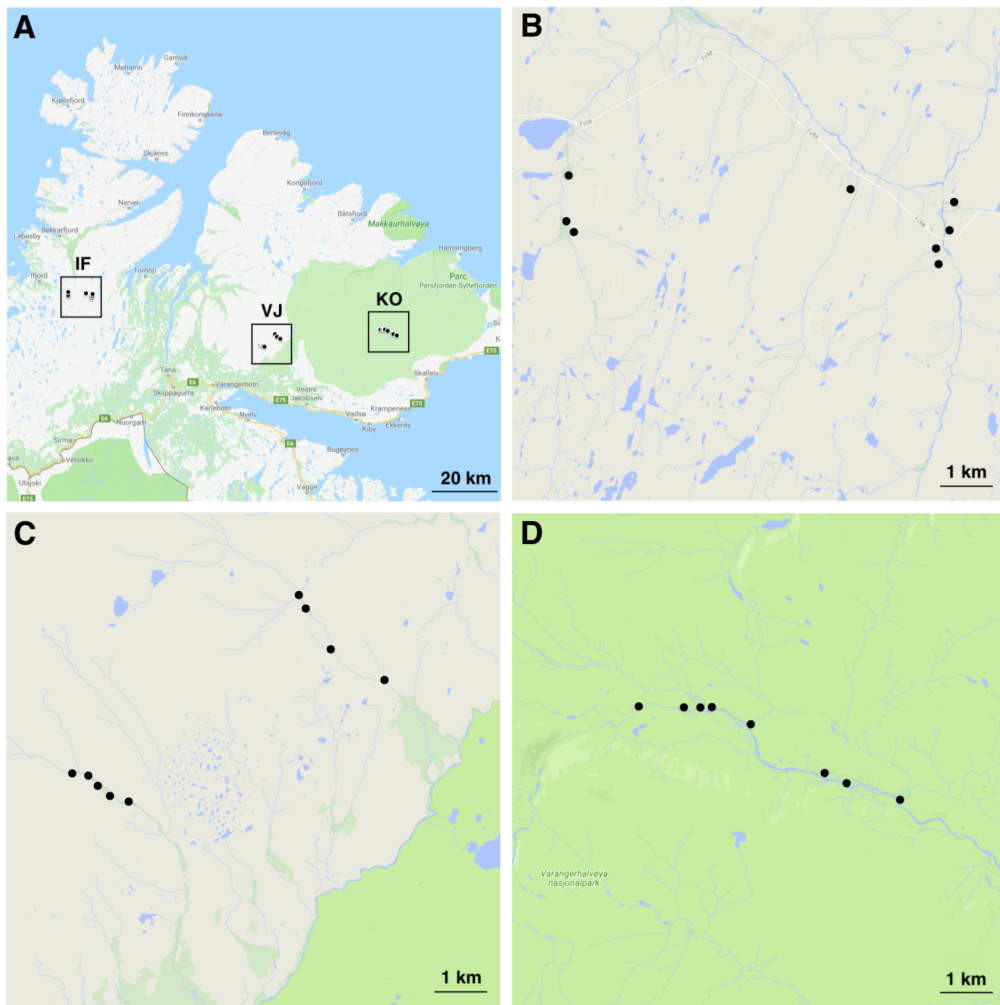
Figure 1: **A)** Map of the Varanger Peninsula (Northern Norway) and location of the three studied regions. **B)**, **C)** and **D)** Maps of the studied regions Ifjord (IF), Komag (KO) and Vestre Jakobselv (VJ) respectively. The black dots indicate the location of the sampling points along the river valleys.

12

Rodent abundance

Three main species of small rodent inhabit the Varanger Peninsula: the tundra vole (*Microtus oeconomus*), the grey-sided vole (*Myodes rufocanus*) and the Norway lemming (*Lemmus lemmus*) [17]. The COAT Team [40] collected rodent abundance by snap-trapping, in accord with the small-quadrat method [24]. A total of twelve traps is placed at each sampling quadrat, with three traps being placed within a 2-meter radius of each corner. The traps are baited with oat flakes and raisins, and placed in front of holes or along rodent runways.

Trapping occurred twice a year, at the beginning of summer (late July from 2005 to 2008, early July since 2009) and at the beginning of autumn (end of August to beginning of September), to the exception of one site in Ifjord where the rodent trapping was discontinued after 2008. In each season, two consecutive trap-nights are carried out and the traps are checked after each night (and reset if a rodent was caught during the night). The number of catches per site is summed over all three species to give a total *rodent abundance* variable.

Onset of spring

The date of the onset of spring was calculated by T. Tveraa in accordance with the method described in [41]. Using remote sensing data collected from the MODIS platform (http://modis-land.gsfc.nasa.gov/vi.html), the Enhanced Vegetation Index (EVI) was obtained as a 16-day composite. The EVI provides an index of plant productivity, and is calculated from surface reflectance as explained in the Equation (1) of the previously mentioned article. Its value increases over the year while the snow melts and the plants bud, and decreases later when leaves are shed and snow covers the vegetation. The evolution of EVI over a year for any given pixel is formulated in Equation (2) of Tveraa's study. For a given pixel, S is defined as the date during spring where the midpoint between the minimum and the maximum estimated values of EVI over the year is reached, such as $\text{EVI}(S) = (\text{EVI}_{max} - \text{EVI}_{min})/2$, and is considered to be the onset of spring. (Note that a second date A presents the same value during the autumn). The *onset of spring* variable for a given year and region is the average of S over all selected pixels in the region. Only good quality pixels of vegetation were used, clouded pixels and pixels corresponding to barren areas or large bodies of water were removed. The *number of days after spring* variable is calculated for each sampling occasion as the difference between the sampling day and the day of spring of the corresponding year and region.

13

2.2 Study Species

Species and ecological traits

Sixteen bird species were included in this analysis. The majority were passerines (Passeriformes), with the exception of one species belonging to the order Accipitriformes (*B. lagopus*), one to the Galliformes (*L. lagopus*), and three to the Charadriiformes (*C. temminckii*, *P. apricaria* and *S. longi-caudus*) (Table 1). Other species such as ducks, crows or waders were occasionally observed but were not included in this study because they were most likely incidental. The selected species rely strongly on the studied habitats (riparian willow thickets and surrounding open tundra) for foraging and/or nesting.

One additional species, the reed bunting (*E. schoeniclus*), was originally included in the analysis, but due to the extreme sparsity of its counts, the model did not converge. It was thus removed from the study, despite its affiliation to shrub thickets and the fact that it is present in the area.

All species are classified as Least Concerned on the IUCN website, except for *A. pratensis* and *T. iliacus* that are classified as Near Threatened since 2015 under the population size decline criterion [18].

Table 1 also shows the favoured strategy of each species for three ecological traits: "migration", "diet" and "habitat use". The classification was done in accordance to information found in natural history databases such as the International Union for Conservation of Nature (IUCN) Red List of Threatened Species [18] and the Handbook of the Birds of the World Alive [8].

The "migration" trait refers to the distance of migration underwent biannually, during spring and autumn. Long distance migrants (N = 6 species) winter in Sub-Saharan Africa or occasionally in southern or eastern Asia, while short-distance migrants (N = 10) winter in Europe, northern Africa or central Eurasia [35]. Species that are resident or for which, during a cold spell, all or parts of the population migrates altitudinally or a few hundred of kilometres only, were grouped with the short-distance migrants.

The "diet" trait describes the favoured food source during breeding season. Insectivores (N = 10 species) mostly prey on invertebrates such as insects and spiders. Herbivores (N = 3) mainly feed on leaves, buds, fruits and seeds. Carnivores (N = 2) mostly prey on small mammals and occasionally on bird eggs and carrion. One species (*T. pilaris*) was classified as omnivorous because of its mixed diet of plants and insects.

The "habitat use" trait designates the favoured breeding habitat. Open tundra species (N = 8 species) nest on the ground in the low vegetation of

14

Table 1: List of studied bird species identified by their scientific name and common English and Norwegian name. The ecological grouping is also indicated depending on their favoured strategy. For the migration strategy : LD = Long-Distance migrants; SD = Short-Distance migrants and residents. For the habitat use : OT = Open Tundra; WCB = Willow Canopy Breeding; WGB = Willow Ground Breeding. For the diet : CA = Carnivorous; HE = Herbivorous; IN = Insectivorous; OM = Omnivorous

			ECOLOGICAL GROUP		
SCIENTIFIC NAME	ENGLISH NAME	NORWEGIAN NAME	Migration	Habitat use	Diet
Anthus cervinus	Red-throated pipit	Lappiplerke	LD	OT	IN
Anthus pratensis	Meadow pipit	Heipiplerke	SD	OT	IN
Buteo lagopus	Rough-legged buzzard	Fjellvåk	SD	OT	CA
Calcarius lapponicus	Lapland longspur	Lappspurv	SD	OT	IN
Calidris temminckii	Temminck's stint	Temmincksnipe	LD	WGB	IN
Carduelis flammea	Redpoll	Gråsisik	SD	WCB	HE
Fringilla montifringilla	Brambling	Bjørkefink	SD	WCB	HE
Lagopus lagopus	Willow grouse	Lirype	SD	WGB	HE
Luscinia svecica	Bluethroat	Blåstrupe	LD	WGB	IN
Motacilla alba	White wagtail	Linerle	SD	OT	IN
Oenanthe oenanthe	Northern wheatear	Steinskvett	LD	OT	IN
Phylloscopus trochilus	Willow warbler	Løvsanger	LD	WGB	IN
Pluvialis apricaria	Eurasian golden plover	Heilo	SD	OT	IN
Stercorarius longicaudus	Long-tailed skua	Fjelljo	LD	OT	CA
Turdus iliacus	Redwing	Rødvingetrost	SD	WCB	IN
Turdus pilaris	Fieldfare	Gråtrost	SD	WCB	OM

open areas. Willow ground-breeding species (N = 4) nest on the ground as well, among the vegetation or between rocks, but under the shelter of tall shrubs. Willow canopy-breeding species (N = 4) build their nest as a cup of vegetation placed high in the willow branches.

The issue of imperfect detection

When studying natural populations of animal species, the issue of imperfect detection arises. Relying on a simple counting method to assess abundance would assume that the detection probability p is perfect ($p = 1$), constant over time ($p_{it} = p_{it+1}$) and space ($p_{it} = p_{jt}$ for sampling locations i and j), and in the case of a community-level study, similar among species ($p_A = p_B$ for species A and B). These assumptions could however be easily violated in many natural situations [21]. Indeed, in order to detect an individual, two conditions must be met: (i) the individual must produce a signal and (ii) the signal must be perceived by an observer. The variability of detection probability is due to a combination of factors affecting either or both of these conditions. In such a wooded habitat, most of the detectable signals will be aural rather than visual [7], hence the production of a signal is mostly determined by the singing rate, which depends on species, time of day, time of year, habitat, proximity to the observer, and intra-specific differences such as breeding stage, social status and health [1, 44, 23]. Then, the detection of this signal mostly depends on the distance between the observer and the bird, which further interacts with background noise, structure of the vegetation, song's intensity and frequency and differences within and between observers in aural acuity and experience [1, 38, 26, 12, 7, 36, 3]. It is consequently almost impossible to count all the individuals present in a given area, or even to be certain of the proportion of individuals that was accounted for. Acknowledging the complexity of factors determining the detection probability of an individual, it seems evident that using raw counts can lead to an underestimation of the true abundance in most situation [30, 21] (however, some study find no improvements of estimates from the inclusion of detection probability [2]). Thus, it will be beneficial to take the probability of detection into account in the sampling process (section 2.3) and in the subsequent data analysis (section 2.4).

2.3 Study Design

Several methods have been developed in the past decades to estimate abundance and the probability of detection simultaneously, such as capture-mark-recapture methods, removal sampling, distance sampling and multiple

observers sampling. These methods can be very informative, but also difficult to implement in the field, especially for large-scale studies : they are costly in time and effort, and are not always adequate for rare species yielding mostly small or null site-specific counts [21, 33]. We used the repeated point count method which is already widely used in bird surveys (e.g., Swiss National Breeding Bird Monitoring Program, North American Breeding Bird Study, Great Backyard Bird Count). It is fast and easy to use, applicable to large-scale studies, it requires almost no disturbance to the studied species and the surrounding habitat, and, when coupled to an adequate data analysis method, it allows to estimate explicitly the detection probability and to have a good precision of abundance estimates even for rare species [34]. This method is based on the principle of spatially and temporally repeated counts. For each sampling occasion ($t = 1, 2, \ldots, T$) at each site ($i = 1, 2, \ldots, R$), the number of unique individuals detected is recorded as n_{it}, giving a matrix of observed counts that comprises many zero and small counts [6] due to small site-specific population size and low detection probability [34, 33]. Considering the overall population as a "meta-population" constituted of each site's "sub-population" allows to deal with the sparsity of the data [9].

In practice, upon arrival at a sampling point, the observer waits 10 to 15 minutes for the wildlife to settle back to a less disturbed state, then records all unique individuals seen or heard in a 100 meters radius area, during a 15-minute sampling period. Sampling is repeated spatially over the sampling points defined previously (Section 2.1) and temporally over three replicates for each sampling year (2005-2008, 2010-2011, 2016). Sampling occurred during two to three consecutive days (cf. Supplement S2 for detailed numbers of replicates per plot and per year) in early July, during the hours considered to be of peak activity for birds in the arctic summer (19:00-23:00 and 01:00-08:00), and in similar weather conditions (little to no wind and rain) [40]. The river valleys are followed in both direction successively, in order to induce an inconsistency in point sampling order, and because true randomisation would be impractical due to the great distance between the sampling points. The sampling was done by two experienced observers (R.A. Ims and G. Vie) over the whole study period[1].

2.4 The generalised N-mixture model

Data obtained from such spatially and temporally repeated counts are currently best analysed with hierarchical models that take into account two

---

[1]during my fieldwork period in the summer of 2016, I did the sampling in Vestre Jakobselv along with G. Vie, but I preferred to consider this as a training and to keep observer consistency by using Vie's data for the analysis.

processes : (i) the state process, determining the true abundance N_i at a site i and (ii) the detection process, determining the observed counts n_i, which are always only a subset of N_i [9]. The true abundance is always latent, it cannot be observed directly because it is only seen through the filter of imperfect detection.

Royle [34] developed a class of hierarchical models (N-mixture models) aimed at analysing data from repeated-point count sampling. However, this model assumes population closure, i.e. no birth, death or migration can occur within the overall population during the whole study period, such as $N_{it} = N_{it+1}$ for any site i at any time t during the study period. It can be useful in many situations (e.g., when the study focuses on the estimation of the total abundance or when the study period spans a single breeding season) but when temporal effects have to be studied, the sampling period will naturally extend over several breeding seasons and the population closure assumption will be violated. The generalisation of this model by Dail and Madsen [6] accommodates for $N_{it} \neq N_{it+1}$, which allows the study of open meta-populations, the estimation of population dynamic parameters (colonisation and extinction rates, growth rate) and the investigation of temporal trends in abundance. This model assumes that (i) individual detections are independent, (ii) all individuals of the same species have the same detection probability at a given site i and sampling occasion t, and (iii) sites are independent.

In accordance with the sampling process described in the previous section, R sites ($i = 1, 2, \ldots, R$) are sampled on T occasions ($t = 1, 2, \ldots, T$). The sampling occasions are furthermore hierarchised into primary periods (years) and secondary periods (replicates within years) which helps to increase the precision of the estimates. However, for the sake of simplicity, this distinction will not be elaborated on in the upcoming formulas. Each sampling event at site i and time t generates an observed count n_{it}, viewed as a realisation of a binomial random variable such as $n_{it} \sim \mathrm{Bin}(N_{it}, p_{it})$ with N_{it} being the true abundance and p_{it} being the detection probability specific to this time and location [21]. The initial latent abundance at site i, N_{i1} is considered as a random variable with a Poisson prior distribution such as $N_{i1} \sim \mathrm{Poisson}(\lambda)$ where λ is the mean abundance during $t = 1$, i.e. the first primary period of the study.

Trends are investigated here as a simple case of exponential growth where N_{it} depends only on N_{it-1} such as $N_{it} = N_{it-1} \times \gamma$ with γ being the finite rate of increase (usually referred to as λ in the literature) [6, 10].

In order to increase the precision of estimates and to investigate relationships between bird species abundance and environmental variables, covariates can be included in the modelling of the parameters with a log link for the

abundance and the growth rate, and with a logit link for the detection probability [6]. The parameters are then estimated through maximisation of the likelihood.

2.5 Data analysis

Status of the bird community

The generalised N-mixture model is implemented in the software R [31] with the function `pcountopen` from the package `unmarked` [9]. All species are modelled with a Poisson prior distribution for the initial abundance, and a simple "trend" dynamic where the growth rate is estimated as the finite rate of increase.

The environmental variables described previously were included as additive covariates in the modelling of the initial abundance (willow area + willow height), the growth rate (rodent abundance + onset of spring) and the detection probability (willow area + willow height + willow density + number of days after spring + year). All of them were scaled and centred to obtain mean = 0 and SD = 1. The original scale was as follow:

– willow area ($\bar{x} = 25.9$ % ; SD = 15.4 %)

– willow height ($\bar{x} = 168$ cm ; SD = 53.7 cm)

– willow density ($\bar{x} = 2.6$ hits ; SD = 1.2 hits)

– rodent abundance ($\bar{x} = 4.9$ individuals ; SD = 4.8 individuals)

– onset of spring ($\bar{x} = 162.9$ days since January 1st ; SD = 9 days)

– number of days after spring ($\bar{x} = 22.5$ days ; SD = 9.7 days)

– year ($\bar{x} = 2009$; SD = 3.5 years).

The estimated parameter are obtained on the log scale for abundance and growth rate, and on the logit scale for detection probability. To obtain the estimates on the linear scale, an exponential back-transformation is applied on the abundance and growth rate estimates, and a logistic transformation is applied on the detection probability estimates.

The function `ranef` allows to estimate the posterior distribution of the random variable, i.e the latent abundance N_{it} for each site i and year t. Averaging these estimation over all sites generates a detailed estimation of yearly fluctuations in abundance. Moreover, combining these values per site or per year provides a crude estimation of species richness per site and site occupancy, globally describing the state of the bird community as a whole.

Effects of environmental temporal variation on bird growth rate

In addition to the global estimates of the growth rate and its associated covariates provided by the model results, the function `predict` returns predicted values of a parameter (here the finite rate of increase γ) for the values taken by a given covariate (here the rodent abundance and the onset of spring). It allows to visualise the relationship between an environmental variable and a biological parameter.

A meta-analysis was performed in order to investigate if some ecological strategies related to migration strategy, habitat use or diet are linked to a higher or lower sensitivity to the effects of rodent abundance and onset of spring. The function `metagen` in the R package `meta` [37] utilises the estimates of the effect of a covariate on a given parameter and its standard error to analyse the effect of a variable on a group of species submitted to the same treatment (here a treatment is considered as an ecological strategy, such as long-distance migrant or short-distance migrant), and allows the comparison of the intensity of the effect on different groupings of species (i.e. treatments).

3 Results

3.1 Ecosystem generalities

Rodent abundance

Rodents exhibit a large year-to-year variability in abundance, with a total number of individuals trapped per year ranging from 10 (in 2009) to 265 (in 2015). During the study period, peak years have been happening every four years (2007, 2011, 2015). The three regions have shown a rather high synchronicity, even if VJ exhibit less clearly defined population cycles (Supplement S1). As shown in Figure 2, the cycle amplitude is largely due to changes in the tundra vole population. The three rodent species show synchronicity in the timing of their respective peak years, but the Norwegian lemming cycles have been dampening over the course of the study period, and, unlike the two vole species, no peak year have been observed in 2011.

Day of spring

The first day of spring varied greatly between years since 2005, starting as early as day 135 (May 15) or as late as day 180 (June 29) (Figure 3). No clear trend towards consistently earlier or later spring can be observed during this time period. The date of onset of spring fluctuates rather synchronously among the three regions, but KO seems to often experience an earlier spring than IF and VJ.

3.2 Status of the bird community

Generalities

The total latent abundance N has been decreasing consistently for seven species over all years, while the other species showed periods of stable or increasing yearly abundance (Supplement S3). *T. pilaris* is the only species to have a larger population in the end than in the beginning of the study. Two species, *B. lagopus* and *L. lagopus*, had a null abundance in 2016. With all species taken together, the total number of birds estimated to be present in the studied area decreased more than two-fold between 2005 ($N = 4969$) and 2016 ($N = 2148$).

The average number of species per site decreased from 15 (range = 14 - 16) in 2005 to 11 (range = 7 - 13) in 2016 (Supplement S4). Similarly, the average number of occupied sites over all species has been decreasing from
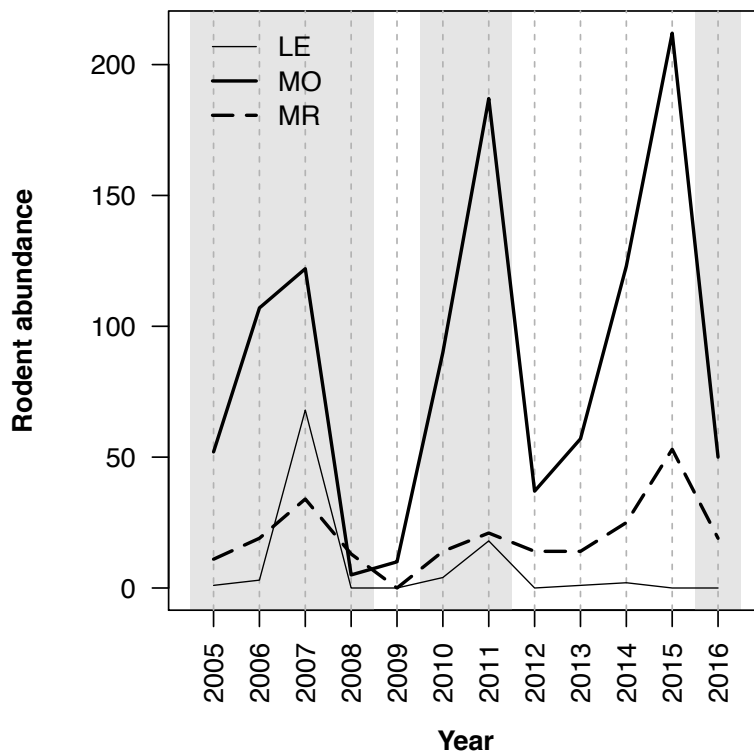
Figure 2: Yearly abundance of three rodent species as a sum over all studied sites. The thin solid line represents the Norway lemming (LE = *Lemmus lemmus*), the thick solid line represents the tundra vole (MO = *Microtus oeconomus*) and the thick dashed line represents the grey-sided vole (MR = *Myodes rufocanus*). Grey areas highlight the years where bird sampling was conducted.
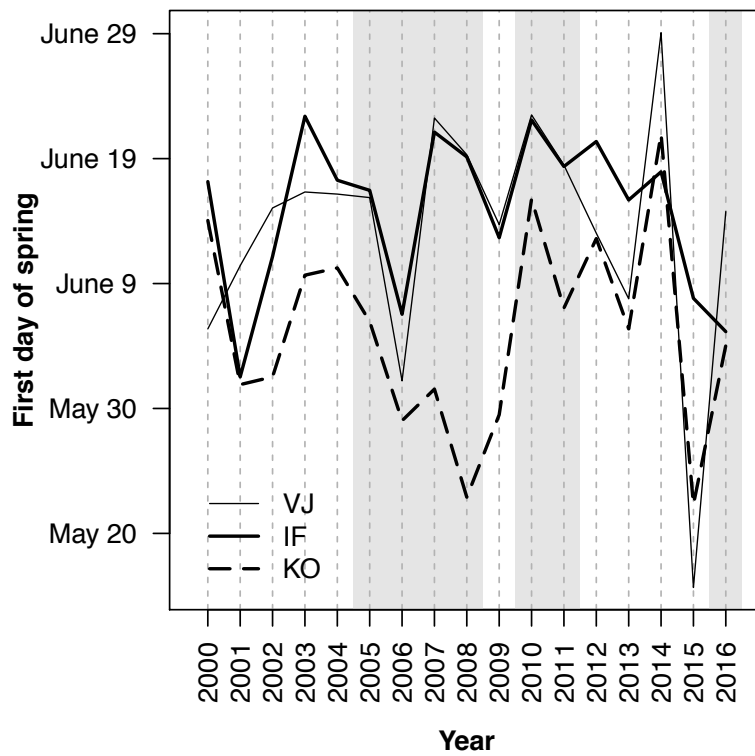
Figure 3: Date of the onset of spring in each of the three studied regions. The thin solid line represents Vestre Jakobselv (VJ), the thick solid line represents Ifjord (IF) and the thick dashed line represents Komag (KO). Grey areas highlight the years where bird sampling was conducted.

Table 2: Estimates of the initial abundance λ, the finite rate of increase γ and the detection probability p. For each parameter, the "Intercept" column gives the estimated value when all the associated covariates are fixed at their mean value. The following columns give the specific effect of a given covariate on the parameter estimated. The values between brackets represent the 95% confidence interval. Values in bold are statistically significant with p-value < 0.05. All values are given on the linear scale, after back-transformation from their original log-scale (for λ and γ) or logit-scale (for p). For λ and γ, covariate values between 0 and 1 indicate a negative effect on the parameter, and values above 1 indicate a positive effect. For p, covariate values between 0 and 0.5 indicate a negative effect on the parameter and values between 0.5 and 1 indicate a positive effect.

SPECIES	INITIAL ABUNDANCE λ			GROWTH RATE γ		
	Intercept	Willow area	Willow height	Intercept	Rodent abundance	Day of spring
A. cervinus	0.151 [0.013 - 1.736]	**0.083** [0.007 - 0.944]	0.664 [0.230 - 1.921]	0.842 [0.611 - 1.160]	1.311 [0.812 - 2.116]	0.827 [0.632 - 1.082]
A. pratensis	**23.268** [15.503 - 34.923]	0.961 [0.649 - 1.423]	0.910 [0.677 - 1.222]	0.949 [0.879 - 1.025]	1.013 [0.974 - 1.055]	0.980 [0.937 - 1.025]
B. lagopus	1.196 [0.289 - 4.949]	0.679 [0.369 - 1.247]	**7.105** [2.812 - 17.951]	**0.552** [0.367 - 0.831]	0.853 [0.474 - 1.533]	1.527 [0.956 - 2.440]
C. lapponicus	**3.812** [1.822 - 7.974]	0.857 [0.464 - 1.583]	0.528 [0.262 - 1.064]	0.927 [0.759 - 1.131]	0.970 [0.867 - 1.084]	1.138 [0.940 - 1.378]
C. temminckii	3.026 [0.008 - 1197.669]	1.029 [0.144 - 7.359]	0.231 [0.004 - 13.960]	0.838 [0.531 - 1.322]	0.969 [0.769 - 1.221]	1.095 [0.600 - 2.000]
C. flammea	**21.952** [14.634 - 32.931]	1.072 [0.867 - 1.324]	1.108 [0.840 - 1.461]	0.952 [0.882 - 1.028]	0.954 [0.910 - 1.000]	0.987 [0.943 - 1.033]
F. montifringilla	10.636 [2.612 - 43.317]	1.794 [0.871 - 3.694]	0.799 [0.355 - 1.795]	0.849 [0.706 - 1.021]	1.040 [0.953 - 1.135]	**0.859** [0.767 - 0.960]
L. lagopus	22.034 [6.078 - 79.872]	1.126 [0.519 - 2.444]	1.014 [0.417 - 2.464]	**0.455** [0.265 - 0.780]	1.056 [0.774 - 1.441]	0.815 [0.622 - 1.069]
L. svecica	17.843 [7.178 - 44.354]	1.266 [0.765 - 2.095]	0.968 [0.553 - 1.694]	0.909 [0.762 - 1.085]	0.998 [0.923 - 1.079]	0.975 [0.905 - 1.051]
M. alba	15.013 [3.983 - 56.595]	1.064 [0.532 - 2.129]	1.094 [0.453 - 2.644]	0.917 [0.753 - 1.116]	1.001 [0.924 - 1.084]	0.943 [0.868 - 1.025]
O. oenanthe	13.168 [2.000 - 86.712]	0.770 [0.233 - 2.548]	0.736 [0.264 - 2.053]	0.907 [0.714 - 1.152]	0.992 [0.872 - 1.128]	1.004 [0.895 - 1.125]
P. trochilus	9.284 [4.464 - 19.309]	**1.552** [1.078 - 2.235]	1.281 [0.792 - 2.071]	0.994 [0.905 - 1.092]	1.008 [0.959 - 1.061]	0.961 [0.908 - 1.016]
P. apricaria	19.264 [5.971 - 62.154]	0.838 [0.330 - 2.127]	0.979 [0.532 - 1.800]	0.880 [0.709 - 1.092]	1.005 [0.917 - 1.102]	0.978 [0.896 - 1.066]
S. longicaudus	6.500 [2.127 - 19.859]	1.970 [0.812 - 4.781]	**0.407** [0.176 - 0.944]	0.841 [0.681 - 1.039]	1.232 [0.973 - 1.561]	**0.854** [0.747 - 0.976]
T. iliacus	6.822 [2.959 - 15.725]	1.315 [0.759 - 2.279]	**0.516** [0.279 - 0.955]	0.881 [0.754 - 1.029]	1.066 [0.970 - 1.173]	1.055 [0.939 - 1.185]
T. pilaris	**3.490** [1.987 - 6.129]	1.464 [0.862 - 2.484]	0.838 [0.528 - 1.329]	0.996 [0.892 - 1.112]	**1.155** [1.031 - 1.295]	**0.879** [0.797 - 0.968]

Continued on next page

24

Table 2 (Continued)

SPECIES	DETECTION PROBABILITY p					
	Intercept	Willow area	Willow density	Willow height	Day after spring	Year
A. cervinus	**0.038** [0.006 - 0.207]	0.640 [0.240 - 0.909]	0.618 [0.392 - 0.802]	**0.163** [0.055 - 0.394]	**0.706** [0.559 - 0.820]	0.542 [0.213 - 0.837]
A. pratensis	**0.058** [0.045 - 0.076]	0.532 [0.430 - 0.632]	0.509 [0.475 - 0.544]	0.533 [0.450 - 0.614]	**0.568** [0.536 - 0.600]	**0.575** [0.511 - 0.636]
B. lagopus	0.390 [0.056 - 0.874]	**0.003** [0.000 - 0.085]	0.398 [0.230 - 0.594]	**0.008** [0.000 - 0.342]	0.433 [0.159 - 0.755]	**1.000** [0.947 - 1.000]
C. lapponicus	**0.068** [0.033 - 0.134]	0.430 [0.291 - 0.582]	**0.639** [0.542 - 0.726]	0.424 [0.256 - 0.611]	0.514 [0.452 - 0.575]	0.461 [0.314 - 0.616]
C. temminckii	0.001 [0.000 - 0.556]	0.740 [0.261 - 0.958]	0.692 [0.187 - 0.957]	0.187 [0.002 - 0.967]	0.569 [0.369 - 0.748]	**0.781** [0.524 - 0.921]
C. flammea	**0.074** [0.057 - 0.094]	**0.584** [0.537 - 0.629]	0.518 [0.480 - 0.555]	0.453 [0.383 - 0.525]	**0.566** [0.536 - 0.595]	0.557 [0.487 - 0.626]
F. montifringilla	**0.003** [0.001 - 0.009]	0.573 [0.367 - 0.757]	0.523 [0.382 - 0.660]	0.704 [0.337 - 0.918]	**0.291** [0.157 - 0.476]	**0.848** [0.720 - 0.924]
L. lagopus	**0.014** [0.001 - 0.187]	0.442 [0.213 - 0.699]	0.624 [0.423 - 0.790]	0.689 [0.309 - 0.917]	0.316 [0.153 - 0.540]	0.931 [0.373 - 0.997]
L. svecica	**0.019** [0.010 - 0.034]	0.488 [0.347 - 0.631]	0.555 [0.488 - 0.621]	0.519 [0.378 - 0.657]	0.496 [0.433 - 0.560]	0.596 [0.436 - 0.738]
M. alba	**0.009** [0.004 - 0.023]	0.356 [0.213 - 0.529]	0.443 [0.381 - 0.506]	0.530 [0.303 - 0.745]	0.567 [0.484 - 0.647]	0.617 [0.438 - 0.768]
O. oenanthe	**0.008** [0.002 - 0.033]	0.424 [0.177 - 0.716]	**0.396** [0.316 - 0.483]	0.549 [0.300 - 0.776]	0.574 [0.480 - 0.663]	0.581 [0.369 - 0.767]
P. trochilus	**0.047** [0.029 - 0.075]	0.519 [0.437 - 0.601]	0.522 [0.463 - 0.581]	0.528 [0.407 - 0.646]	0.534 [0.488 - 0.579]	0.547 [0.464 - 0.628]
P. apricaria	**0.008** [0.003 - 0.022]	0.451 [0.233 - 0.689]	0.559 [0.476 - 0.639]	0.370 [0.236 - 0.528]	0.548 [0.464 - 0.629]	0.667 [0.482 - 0.811]
S. longicaudus	**0.010** [0.004 - 0.025]	0.319 [0.137 - 0.581]	0.586 [0.455 - 0.705]	0.411 [0.230 - 0.620]	0.534 [0.415 - 0.650]	0.605 [0.460 - 0.735]
T. iliacus	**0.093** [0.057 - 0.149]	0.463 [0.346 - 0.585]	0.435 [0.357 - 0.516]	**0.718** [0.561 - 0.836]	0.499 [0.442 - 0.556]	0.547 [0.411 - 0.677]
T. pilaris	**0.072** [0.047 - 0.107]	0.483 [0.371 - 0.596]	**0.345** [0.281 - 0.415]	0.489 [0.363 - 0.615]	0.554 [0.496 - 0.610]	**0.389** [0.303 - 0.483]

23 (range = 10 - 25) in 2005 to 17 (range = 0 - 25) in 2016 (Supplement S5). Most species showed period of decreasing occupancy, but six species have been occupying all of the 25 sites throughout the course of the study. Despite their maximum occupancy, four of these six species (*L. svecica, M. alba, O. oenanthe* and *P. apricaria*) are among the ones that experienced consistent decreases in abundance despite their maximum occupancy.

The estimated mean initial abundance λ varied greatly among species, ranging from a couple of individuals per site to more than 20. Willow area had a statistically significant ($p < 0.05$) large positive effect on *P. trochilus* initial abundance and a very slight negative effect on *A. cervinus* initial abundance. For the other species, the direction of the effect was unclear. Similarly, willow height had a statistically significant large positive effect on *B. lagopus*, and a rather large negative effect on *S. longicaudus* and *T. iliacus*.

The significant detection probability varied from 0.3% to 9.3% per visit, with a mean of 3.7%.

Population dynamic of the bird species

Out of the 16 species, only two species, the rough-legged buzzard (*B. lagopus*) and the willow grouse (*L. lagopus*) showed a finite rate of increase $\gamma < 1$ over the whole study period that was statistically significant ($p < 0.05$) (Table 2). When the covariates are fixed at their mean value, $\gamma_{B.lagopus} = 0.552$ [95% CI = 0.367 ; 0.831] and $\gamma_{L.lagopus} = 0.455$ [95% CI = 0.265 ; 0.780] on the linear scale. This suggest a negative population trend, with the abundance being roughly halved every year. As indicated in Figure 4 and Supplement S3, the two species reached an estimated population size of zero towards the end of the study. All the other species had a growth rate estimate such as $\gamma < 1$, but the estimation was not statistically significant, and the 95% confidence interval spanned values below and above 1, which suggest the absence of a detectable trend in population abundance.

The mean latent abundance N_{it} for site i and year t show some year-to-year variations (Figure 4). In accordance with Table 2 and Supplement S3, *B. lagopus* and *L. lagopus* show a negative exponential growth rate, with a narrow 95% confidence interval. Five other species (*C. temminckii, L. svecica, M. alba, O. oenanthe* and *P. apricaria*) showed a consistently decreasing N_{it} but the 95% confidence interval was too wide to conclude statistically on the presence of a decreasing trend. The remaining nine species showed periods of stable or increasing mean population size.
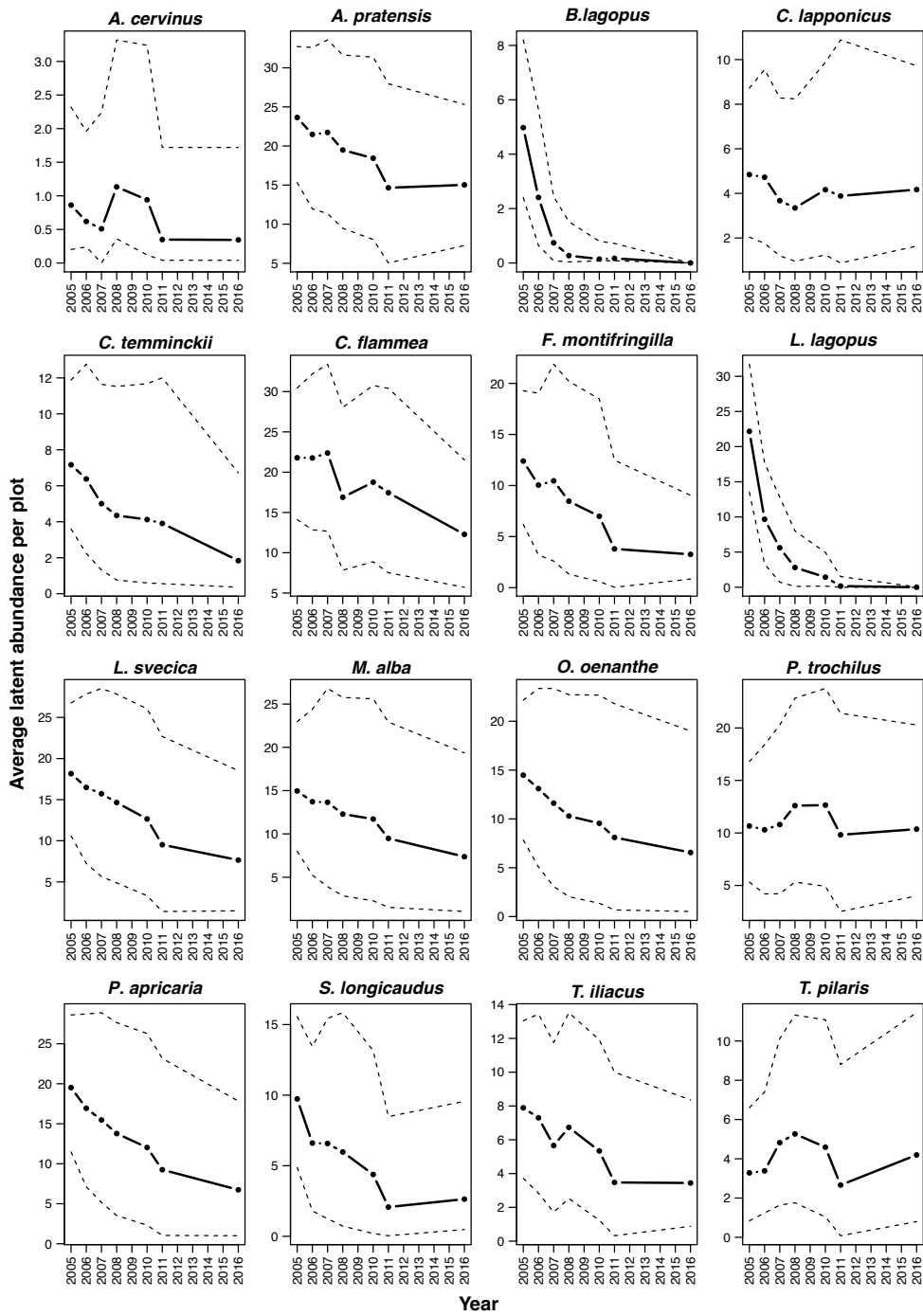
26

Figure 4: Estimation of the yearly latent abundance N_i as a mean over all plots. The dashed line indicates the mean 95% confidence interval. Bird sampling did not occur during the years 2009 and 2012 to 2015.

3.3 Effect of temporal variation on the bird community

According to Table 2, the rodent abundance had a significant positive effect on the growth rate of *T. pilaris* with an estimate of 1.155, and an unclear effect on the other species. The effect of the rodent abundance on the growth rate is given for one standard deviation of the covariate (i.e. the addition of 4.8 individuals to a sampling location), which would result in an increase in growth rate by 15.5%. The range of rodent abundance variation between crash and peak years is rather large, with an abundance that differs by two-fold, three-fold or more in two consecutive years. The effect size of the covariate on the growth rate will depend on the amplitude of the rodent population cycles. Figure 5 shows the predicted effect of the rodent abundance on the growth rate, but for most species the predictions are too scattered to draw any reliable conclusion.

A later day of spring had a significant negative effect on the growth rate of *S. longicaudus*, *F. montifringilla*, and *T. pilaris*, with estimate values at 0.854, 0.859 and 0.879 respectively. The covariate estimate is given for one standard deviation, which in this case represents a spring delayed by 9 days. The effect on the three species is similar, with a decrease in growth rate of about 12 to 15% for spring in such way. Figure 6 shows the predicted effect of the date of spring on the bird growth rate. The predictions seem to be too scattered to observe a clear pattern. However, it seems like some species (e.g., *B. lagopus*, *C. lapponicus*, *C. temminckii*, *T. iliacus*) exhibit a lower growth rate for low and high values of onset of spring, and higher growth rate predictions for average onset of spring.

3.4 Sensitivity of different ecological groups

The two species exhibiting a strong negative population trend belonged to the same ecological grouping of short-distance migrants or residents. However, *B. lagopus* is a truly open tundra species while *L. lagopus* is a willow-ground breeder. Similarly, *B. lagopus* is carnivorous while *L. lagopus* is herbivorous. The five species mentioned previously with no significant negative growth rate but seemingly decreasing overall latent abundance were all insectivorous, but belonged to various ecological groups for migration and habitat use : three long-distance and two short-distance migrants, two willow-canopy breeding species and three open tundra species.

According to Table 3, a later spring seems to have a slightly more negative effect on long-distance migrants than short-distance migrants and resident species, with -0.044 (CI = -0.083 ; -0.004) and -0.030 (CI = -0.056 ; -0.005)
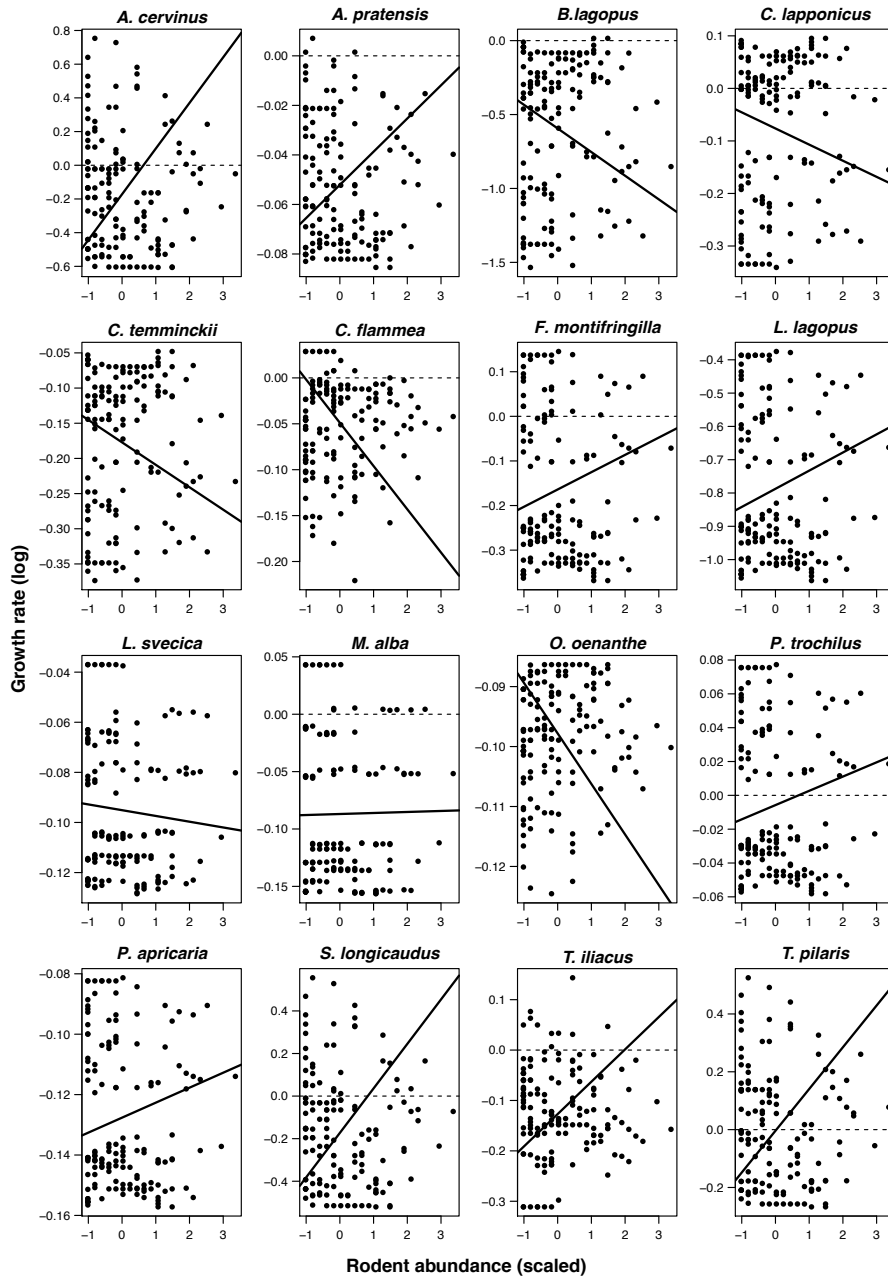
Figure 5: Predicted effect of rodent abundance (scaled) on the bird species growth rate (log scale). Each point represents the growth rate at a year.site combination. As the growth rate is calculated based on the abundance of the previous year, no growth rate estimate is available for the year 2005.The horizontal dashed line represents $\gamma = 0$, where the growth rate is null. The bold solid line represents the prediction of the effect, from the model estimates.
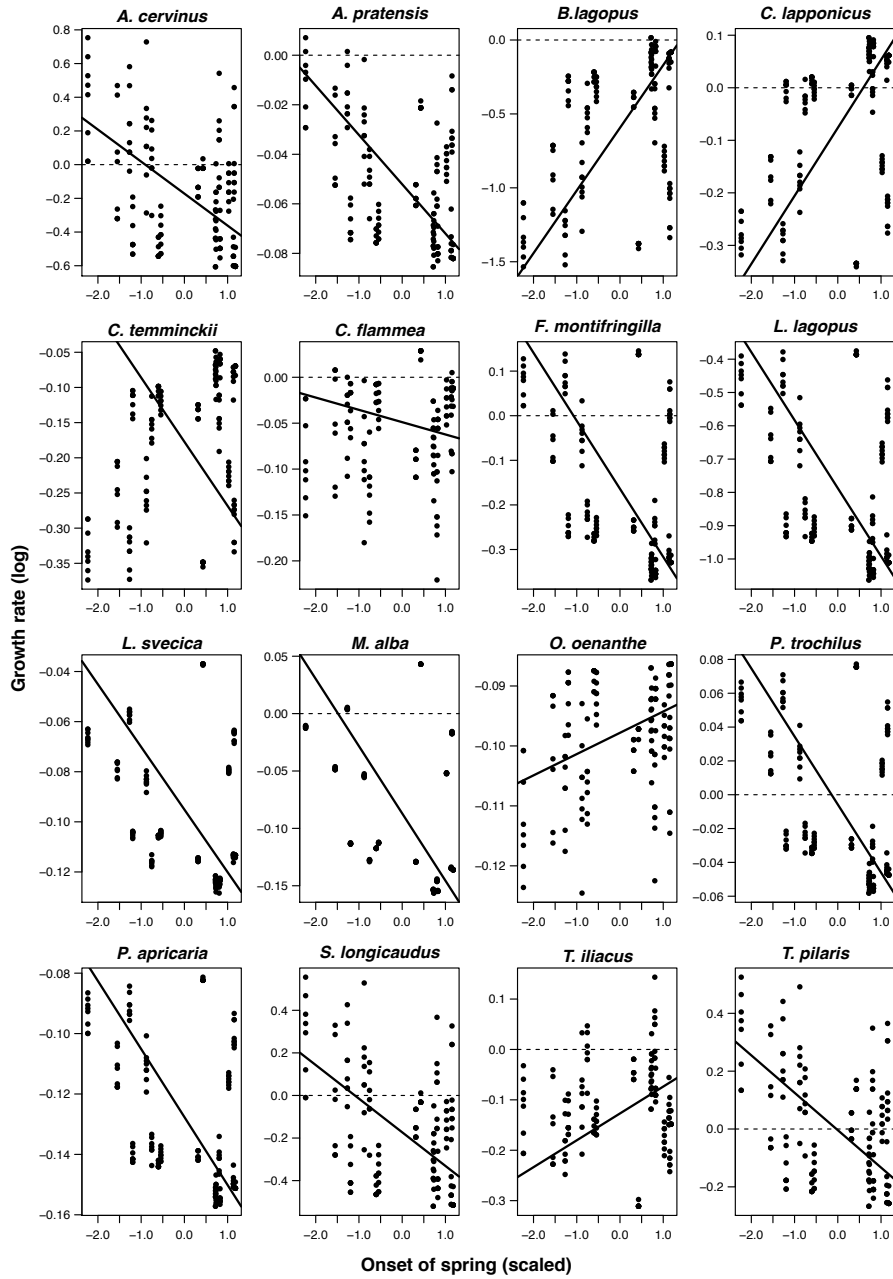
Figure 6: Predicted effect of the date of onset of spring (scaled) on the bird species growth rate (log scale). Each point represents the growth rate at a year.site combination. As the growth rate is calculated based on the abundance of the previous year, no growth rate estimate is available for the year 2005. The horizontal dashed line represents $\gamma = 0$, where the growth rate is null. The bold solid line represents the prediction of the effect, from the model estimates.

respectively, but the difference is not large enough to draw conclusions. It also appears to have a more positive effect on willow-related species than on open tundra species, but the results were not significant.

An increased rodent abundance affects positively species linked to the willow thicket. The effect on other ecological traits was not significant.

Table 3: Results of the meta-analysis showing the specific effect of the rodent abundance and the onset of spring covariates on the bird species growth rate. Values between brackets show the 95% confidence interval. The values in bold are statistically significant ($p < 0.05$). LD = Long-Distance migrants; SD = Short-Distance migrants and residents. OT = Open Tundra; WCB = Willow Canopy Breeding; WGB = Willow Ground Breeding. HE = Herbivorous; IN = Insectivorous

ECOLOGICAL TRAIT	CATEGORY	RODENT ABUNDANCE		ONSET OF SPRING	
Migration	LD	0.010	[-0.029 ; 0.049]	**-0.044**	[-0.083 ; -0.004]
	SD	0.005	[-0.019 ; 0.029]	**-0.030**	[-0.056 ; -0.005]
Habitat use	OT	-0.089	[-0.330 ; 0.152]	-0.090	[-0.304 ; 0.123]
	WGB	**0.334**	[0.058 ; 0.605]	0.101	[-0.225 ; 0.438]
	WCB	0.158	[-0.021 ; 0.338]	0.197	[-0.017 ; 0.410]
Diet	IN	0.010	[-0.014 ; 0.034]	-0.023	[-0.049 ; 0.003]
	HE	-0.026	[-0.067 ; 0.015]	-0.037	[-0.079 ; 0.005]

4 Discussion

Bird community summary

The bird community of the studied region appears to have experienced a general deterioration since 2005. The total abundance of birds all species combined, the average number of occupied sites and the average species richness per site have all been decreasing over the study period. More precise community estimation might be achieved through the use of models targeted at community-level metrics such as species richness or occupancy [20], but these results provide nonetheless an insight on the general status of the bird community as a whole.

Population trends

The rough-legged buzzard (*B. lagopus*) and the willow grouse (*L. lagopus*) showed an important decreasing trend over the study period, with a population being roughly halved every year, to the point of having a null estimated abundance in the last year of study. None of the other species exhibited a clear trend in abundance. Despite this, detailed year-to-year changes in abundance show that some species had a consistently decreasing population abundance while other experienced periods of stable or increasing population size.

Considering population dynamics different than the simple exponential growth might help to identify more complex dynamics such as density-dependence or non linear trends in population size. Investigating prior distributions for the latent abundance different than the Poisson distribution might also increase the precision of the estimates, for example if some species tend to aggregate instead of having a uniform spatial distribution, the negative binomial distribution would be more adapted [34]. Additionally, even though this type of models is supposedly adapted for populations with low counts [34], the fact that the reed bunting (*E. schoeniclus*) population was unsuccessfully modelled suggests that extremely rare species might be poorly studied. This is problematic for species existing in the habitat at extremely low density, but also for the new species that are expected to extend their boreal range to more Arctic systems and that will probably have very low population sizes at the beginning of their colonisation.

Effects of temporal variation

The onset of spring based on vegetation greenness in the studied region does not exhibit a clear change towards earlier spring, but it shows large year-to-year variations. In more Arctic regions, onset of spring have been happening earlier by roughly 14 days/decade [13], while the average advancement in phenologies is much lower on a global scale [28]. It is possible that our 16-year study period for the onset of spring is still too short, compared to the high short-term fluctuations, to observe clear long-term temporal trends.

A spring delayed by 9 days resulted in a predicted growth rate reduced by roughly 14% for three species, suggesting that these species would have a higher growth rate if the predictions of an earlier spring would become effective. Also, it seems that some species might experience a non-linear effect of the onset of spring on their growth rate. Investigating a quadratic relationship between the bird population and the date of spring could reveal different patterns of response to climate change.

Rodent abundance as a whole as been experiencing typical 4-year cycles. However, most of the dynamic is attributable to the tundra vole, and the Norway lemming population has showed dampening cycles consistent with previous studies [17, 11] and an extremely low, if not null, population size since 2012. A part of this dynamic can be explained through a bias in bait attraction, with lemming being less attracted than the tundra vole by the oats and raisins bait, thus leading to an underestimation of the relative population size of the lemming compared to the tundra vole. The grey-sided vole might also be underestimated because it is more associated to the surrounding heaths than the studied meadows.

It is surprising that *B. lagopus* showed no clear response from the rodent dynamic. We can suspect that the observed negative trend started before 2005 and that it is due to environmental changes happening prior the beginning of this study. Thus, rodent peaks in the recent years might have been insufficient to help this carnivorous species to retrieve a sustainable population size.

Sensitivity of different ecological traits

The two species experiencing a clear negative trend, *B. lagopus* and *L. lagopus*, both belonged to the grouping of short-distance migrant and resident species. This is in accordance to previous studies on Scandinavian birds [22]. While long-distance migrants are often expected to be more vulnerable due to the risks linked to this long biannual journey and to the fact that they rely on different habitat undergoing various pressure in different parts of

the world, some birds more tightly linked to Scandinavian habitats seem to perform more poorly.

No clear trend related to the habitat use was observed, despite predictions suggesting that willow related species would thrive in a climate change context while open tundra species would loose ground. However, as the thickets structure is controlled by climate change (favouring shrub encroachment) and herbivore browsing (controlling shrub expansion), it is possible that the studied regions did not experience any major change in habitat structure in the past decade.

Except those two species, all the species exhibiting a consistently decreasing estimated abundance were insectivorous. This might suggest that insectivorous species perform more poorly than species with another diet strategy. However, the fact that most of the species studied belonged to the insectivorous grouping (10 out of 16 species) leads to caution when interpreting a pattern that might only be coincidental. Additionally, the prediction according to which species with the most varied diet would perform better is not refuted, with *T. pilaris*, the only species categorised as omnivorous being also the only species with an increased estimated population size at the end of the study period. A possible explanation would be that some level of phenological mismatch is happening between bird species and their source of food (possibly insects), leading to a decrease in the population size and growth rate of species unable to track such changes. But this is highly speculative and it would require further study to assess the phenology of bird species and insects in this ecosystem. Moreover, different insect taxa show different level of climate-sensitivity [29], and considering with more details the diet of the bird species could lead to more precise expectations concerning future trends and a better understanding of the food-web functioning under environmental change conditions.

Future prospects

Monitoring will continue in the future, with a bird sampling every five years. Detailed year-to-year changes in population size will not be available, but long-term trends will probably become more clearly identifiable with a longer time-series. The investigation of ecological traits is advised to continue, as it can indicate ongoing ecosystem changes. For example, differential trends in the population of open tundra species and willow related species can indicate shifts in the state of the riparian willow thicket habitat, in the balance between thicket fragmentation and shrub-encroachment [32, 17]. It would be beneficial to re-assess regularly the willow variables used in this study, in order to track directly changes in the habitat structure. Also, the

use of a model capable to handle very rare species might help to detect the early appearance of new boreal species that are expected to extend their range northwards.

Additional research should probably focus on the study of phenological trends for the arrival of migratory bird, the breeding timing of the community and the phenology of the insect population. These parameters would inform on possible changes in the timing of spring events and allow to predict the future of bird species, depending on their ability to track such ecosystem changes.

5   Conclusion

The riparian bird community of the Norwegian low-Arctic tundra has been experiencing decreases in total bird abundance, site occupancy and average species richness since 2005. The rough-legged buzzard and the willow grouse showed significant negative trends leading to an estimated null abundance in the most recent years. Most other species displayed signs of population decrease, but without clear discernible population trends. There were no clear environmental trends indicating a long-term change in the onset of spring or a loss of rodent cycles. Three species were found to benefit from an earlier spring. Short-distance migrants and insectivorous species seemed to be experiencing more negative trends than species displaying other ecological strategies. Monitoring will need to continue in the coming years to track the evolution of the bird species abundances and the eventual directional changes in environmental conditions.

Bibliography

[1] Mathew W. Allredge, Theodore R. Simons, and Kenneth H. Pollock. Factors affecting aural detections of songbirds. *Ecological Applications*, 17(3):948–955, 2007.

[2] Yves Bas, Vincent Devictor, Jean-Pierre Moussus, and Frédéric Jiguet. Accounting for weather and time-of-day parameters when analysing count data from monitoring programs. *Biodiversity and Conservation*, 17(14):3403–3416, December 2008.

[3] Thierry Boulinier, James D. Nichols, John R. Sauer, James E. Hines, and K. H. Pollock. Estimating Species Richness: The Importance of Heterogeneity in Species Detectability. *Ecology*, 79(3):1018, April 1998.

[4] S. H. M. Butchart, M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter, G. M. Carr, J. Chanson, A. M. Chenery, J. Csirke, N. C. Davidson, F. Dentener, M. Foster, A. Galli, J. N. Galloway, P. Genovesi, R. D. Gregory, M. Hockings, V. Kapos, J.-F. Lamarque, F. Leverington, J. Loh, M. A. McGeoch, L. McRae, A. Minasyan, M. H. Morcillo, T. E. E. Oldfield, D. Pauly, S. Quader, C. Revenga, J. R. Sauer, B. Skolnik, D. Spear, D. Stanwell-Smith, S. N. Stuart, A. Symes, M. Tierney, T. D. Tyrrell, J.-C. Vie, and R. Watson. Global Biodiversity: Indicators of Recent Declines. *Science*, 328(5982):1164–1168, May 2010.

[5] B. E. N. Collen, Jonathan Loh, Sarah Whitmee, Louise McRae, Rajan Amin, and Jonathan EM Baillie. Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology*, 23(2):317–327, 2009.

[6] D. Dail and L. Madsen. Models for Estimating Abundance from Repeated Counts of an Open Metapopulation. *Biometrics*, 67(2):577–587, June 2011.

[7] Michael J. Dejong and John T. Emlen. The shape of the auditory detection function and its implications for songbird censusing. *Journal of Field Ornithology*, pages 213–223, 1985.

[8] J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, and E. de Juana. Handbook of the Birds of the World Alive, December 2016.

[9] Ian Fiske and Richard Chandler. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10), 2011.

[10] Ian Fiske, Richard B. Chandler, David Miller, Andy Royle, Marc Kéry, Jeffrey A. Hostetler, and Rebecca Hutchinson. Package "unmarked" : Models for Data from Unmarked Animals, May 2017.

[11] John-André Henden, Rolf A Ims, and Nigel G Yoccoz. Nonstationary spatio-temporal small rodent dynamics: evidence from long-term norwegian fox bounty data. *Journal of Animal Ecology*, 78(3):636–645, 2009.

[12] John-André Henden, Nigel G. Yoccoz, Rolf A. Ims, and Knut Langeland. How Spatial Variation in Areal Extent and Configuration of Labile Vegetation States Affect the Riparian Bird Community in Arctic Tundra. *PLoS ONE*, 8(5):e63312, May 2013.

[13] Toke T Høye, Eric Post, Hans Meltofte, Niels M Schmidt, and Mads C Forchhammer. Rapid advancement of spring in the high arctic. *Current Biology*, 17(12):R449–R451, 2007.

[14] R. A. Ims, J.-A. Henden, A. V. Thingnes, and S. T. Killengreen. Indirect food web interactions mediated by predator-rodent dynamics: relative roles of lemmings and voles. *Biology Letters*, 9(6):20130802–20130802, October 2013.

[15] Rolf A Ims and EVA Fuglei. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience*, 55(4):311–322, 2005.

[16] Rolf A. Ims and John-André Henden. Collapse of an arctic bird community resulting from ungulate-induced loss of erect shrubs. *Biological conservation*, 149(1):2–5, 2012.

[17] Rolf A. Ims, Jane U. Jepsen, Audun Stien, and Nigel G. Yoccoz. *Science plan for COAT: climate-ecological observatory for Arctic Tundra*. Fram Centre Report Series 1, Fram Centre, Norway. Fram Centre by the University of Tromsø, 2013.

[18] IUCN. The IUCN Red List of Threatened Species. Version 2017-1, January 2017.

[19] Vladimir M Kattsov, Erland Källén, Howard P Cattle, Jens Christensen, Helge Drange, Inger Hanssen-Bauer, Tómas Jóhannesen, Igor Karol, Jount Räisänen, Gunilla Svensson, et al. Future climate change: modeling and scenarios for the arctic. *Arctic Climate Impact Assessment*, 2005.

[20] M. Kéry and J. A. Royle. Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, 45(2):589–598, April 2008.

[21] Marc Kéry, J. Andrew Royle, and Hans Schmid. Modeling avian abundance from replicated counts using binomial mixture models. *Ecological applications*, 15(4):1450–1461, 2005.

[22] Aleksi Lehikoinen, Martin Green, Magne Husby, John Atle Kålås, and Åke Lindström. Common montane birds are declining in northern Europe. *Journal of Avian Biology*, 45(1):3–14, January 2014.

[23] W.J. McShea and J.H. Rappole. Variable Song Rates in Three Species of Passerines and Implications for Estimating Bird Populations. *Journal of Field Ornithology*, 68(3):367–375, 1997.

[24] Arvo Myllymäki, Arja Paasikallio, Erkki Pankakoski, and Veikko Kanervo. Removal experiments on small quadrats as a means of rapid assessment of the abundance of small mammals. *Annales Zoologici Fennici*, 8(1):177–185, 1971.

[25] A. P. Møller, Wolfgang Fiedler, and P. Berthold, editors. *Effects of climate change on birds*. Oxford University Press, Oxford ; New York, 2010.

[26] Krishna Pacifici, Theodore R. Simons, and Kenneth H. Pollock. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *The Auk*, 125(3):600–607, July 2008.

[27] Camille Parmesan. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 37(1):637–669, December 2006.

[28] Camille Parmesan and Gary Yohe. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918):37–42, 2003.

[29] Jw Pearce-Higgins. Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research*, 45:119–130, December 2010.

[30] Kenneth H. Pollock, James D. Nichols, Theodore R. Simons, George L. Farnsworth, Larissa L. Bailey, and John R. Sauer. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics*, 13(2):105–119, 2002.

[31] R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2017.

[32] Virve Tuulia Ravolainen, Kari Anne Bråthen, Rolf Anker Ims, Nigel Gilles Yoccoz, John-André Henden, and Siw T. Killengreen. Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic and Applied Ecology*, 12(8):643–653, 2011.

[33] J. Andrew Royle. Generalized estimators of avian abundance from count survey data. *Animal Biodiversity and Conservation*, 27(1):375–386, 2004.

[34] J. Andrew Royle. N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, 60(1):108–115, 2004.

[35] Fiona J. Sanderson, Paul F. Donald, Deborah J. Pain, Ian J. Burfield, and Frans P.J. van Bommel. Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, 131(1):93–105, July 2006.

[36] John R. Sauer, Bruce G. Peterjohn, and William A. Link. Observer Differences in the North American Breeding Bird Survey. *The Auk*, 111(1):50–62, January 1994.

[37] Guido Schwarzer. Meta: an r package for meta-analysis. *R news*, 7(3):40–45, 2007.

[38] Theodore R. Simons, Mathew W. Allredge, Kenneth H. Pollock, and John M. Wettroth. Experimental analysis of the auditory detection process on avian point counts. *The Auk*, 124(3):986–999, 2007.

[39] CAVM Team. Circumpolar Arctic vegetation map. Conservation of Arctic Flora and Fauna (CAFF) Map No. 1, 2003.

[40] COAT Team. COAT Varanger field protocol intensive study design (Unpublished), 2016.

[41] Torkild Tveraa, Audun Stien, Bård-J. Bårdsen, and Per Fauchald. Population Densities, Vegetation Green-Up, and Plant Productivity: Impacts on Reproductive Success and Juvenile Body Mass in Reindeer. *PLoS ONE*, 8(2):e56450, February 2013.

[42] Donald A. Walker, Martha K. Raynolds, Fred J. A. Daniëls, Eythor Einarsson, Arve Elvebakk, William A. Gould, Adrian E. Katenin, Sergei S. Kholod, Carl J. Markon, Evgeny S. Melnikov, Natalia G. Moskalenko, Stephen S. Talbot, Boris A. Yurtsev, and CAVM Team. The Circumpolar Arctic Vegetation Map. *Journal of Vegetation Science*, 16(3):267–282, 2005.

[43] Gian-Reto Walther, Eric Post, Peter Convey, Annette Menzel, Camille Parmesan, Trevor J. C. Beebee, Jean-Marc Fromentin, Ove Hoegh-Guldberg, and Franz Bairlein. Ecological responses to recent climate change. *Nature*, 416(6879):389–395, 2002.

[44] David M. Wilson and Jonathan Bart. Reliability of Singing Bird Surveys: Effects of Song Phenology during the Breeding Season. *The Condor*, 87(1):69–73, February 1985.

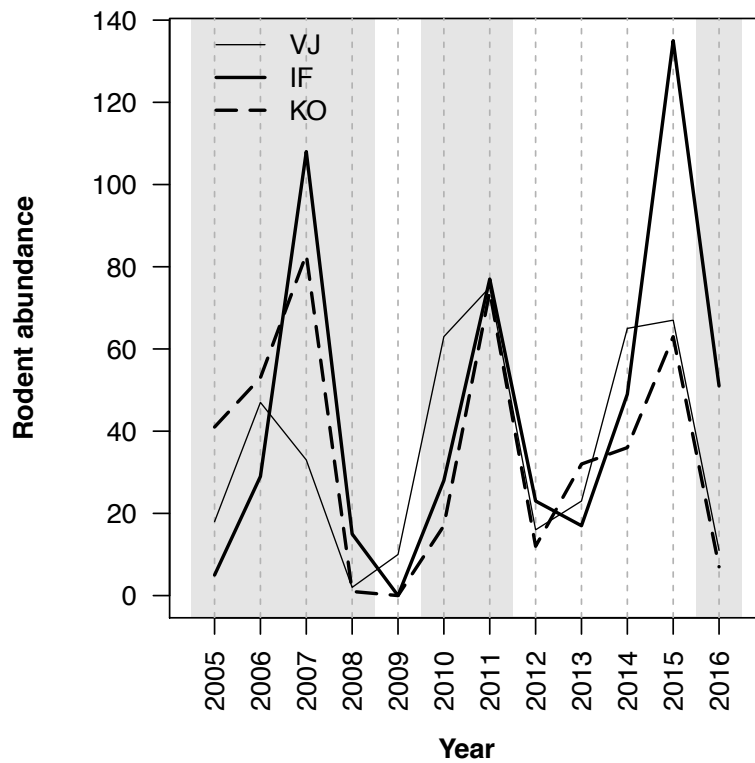# Supplementary material

Figure S1: Combined yearly abundance of the three rodent species (Norway lemming, tundra vole and grey-sided vole) as a sum over all the sites of each region. The thin solid line represents Vestre Jakobselv (VJ), the thick solid line represents Ifjord (IF) and the thick dashed line represents Komag (KO). Grey areas highlight the years where bird sampling was conducted.

Table S2: Number of replicates per year for each sampling point of the three studied regions. The goal was to carry out three replicates per year for each sampling point, over a couple of consecutive days in early July. The occasions where this goal was not achieved are indicated in bold letters.

Region	Sampling point	2005	2006	2007	2008	2010	2011	2016
IF	AE3K	3	3	3	3	**2**	3	3
	AE4K	3	3	3	3	**2**	3	3
	AE5K	3	3	3	3	**2**	3	3
	GU1K	3	3	3	3	**0**	**0**	3
	ST1K	3	3	3	3	**2**	3	3
	ST2K	3	3	3	3	**0**	**0**	3
	ST3K	3	3	3	3	**0**	**0**	3
	ST4K	3	3	3	3	**2**	**0**	3
KO	KOF1A	3	3	3	3	**2**	3	3
	KOF1B	3	3	3	3	**2**	3	3
	KOF1C	3	3	3	3	**2**	3	3
	KOF1D	3	3	3	3	**2**	3	3
	KOF1E	3	3	3	3	**2**	3	3
	KOF2A	3	3	3	3	**0**	**0**	3
	KOF2B	3	3	3	3	**0**	**0**	3
	KOF2E	3	3	**2**	3	**0**	**0**	3
VJ	VJF1A	3	3	3	3	3	3	3
	VJF1B	3	3	3	3	3	3	3
	VJF1C	3	3	3	3	3	3	3
	VJF1D	3	3	3	3	3	3	3
	VJF2A	3	3	3	3	3	3	3
	VJF2B	3	3	3	3	3	3	3
	VJF2C	3	3	3	3	3	3	3
	VJF2D	3	3	3	3	3	3	3
	VJF2E	3	3	3	3	3	3	3

Table S3: Total number of individual per species summed over all sampling site, based on the estimated latent abundance N_{it}.

Species	2005	2006	2007	2008	2010	2011	2016	**Mean**
A. cervinus	22	15	13	28	24	9	9	**17**
A. pratensis	591	537	543	487	461	366	376	**480**
B. lagopus	124	60	19	7	4	4	0	**31**
C. flammea	545	544	559	422	469	436	307	**469**
C. lapponicus	121	118	92	84	104	97	104	**103**
C. temminckii	179	159	125	109	103	98	46	**117**
F. montifringilla	310	251	261	212	175	95	82	**198**
L. lagopus	554	242	140	70	36	4	0	**149**
L. svecica	454	412	393	366	316	238	191	**339**
M. alba	374	343	341	307	293	237	184	**297**
O. oenanthe	362	328	290	257	239	203	164	**263**
P. apricaria	488	423	387	344	301	231	169	**335**
P. trochilus	267	258	270	315	316	246	259	**276**
S. longicaudus	243	165	164	149	110	52	66	**136**
T. iliacus	197	182	141	168	133	87	86	**142**
T. pilaris	82	85	121	132	115	67	105	**101**
Total	**4913**	**4122**	**3859**	**3457**	**3199**	**2470**	**2148**	

Table S4: Total number of species per sampling site, based on the estimated latent abundance N_{it}.

Site	2005	2006	2007	2008	2010	2011	2016	**Mean**
AE3K	14	14	14	13	13	12	12	**13**
AE4K	15	15	15	13	13	12	12	**14**
AE5K	14	14	14	14	14	13	13	**14**
GU1K	14	14	14	14	14	13	12	**14**
KOF1A	16	15	14	13	13	10	9	**13**
KOF1B	16	16	16	14	14	11	12	**14**
KOF1C	16	16	15	13	13	13	12	**14**
KOF1D	14	14	14	14	14	12	12	**13**
KOF1E	15	13	14	11	12	10	9	**12**
KOF2A	14	14	13	13	12	12	10	**13**
KOF2B	14	14	13	12	12	12	10	**12**
KOF2E	15	14	14	12	12	11	10	**13**
ST1K	15	14	14	14	14	13	11	**14**
ST2K	14	14	14	14	14	13	13	**14**
ST3K	15	15	15	15	15	14	12	**14**
ST4K	14	15	15	15	15	13	12	**14**
VJF1A	16	16	16	16	15	11	9	**14**
VJF1B	15	15	14	14	13	13	10	**13**
VJF1C	15	14	14	14	13	13	11	**13**
VJF1D	15	14	14	14	13	13	12	**14**
VJF2A	16	16	15	14	12	9	7	**13**
VJF2B	14	14	14	14	14	13	12	**14**
VJF2C	15	15	14	14	13	12	12	**14**
VJF2D	15	15	14	13	13	12	11	**13**
VJF2E	15	15	14	14	14	14	12	**14**
Mean	**15**	**15**	**14**	**14**	**13**	**12**	**11**	

Table S5: Total number of sites occupied per year for each species, based on the estimated latent abundance N_{it}.

Species	2005	2006	2007	2008	2010	2011	2016	**Mean**
A. cervinus	10	8	7	7	8	4	3	**7**
A. pratensis	25	25	25	25	25	25	25	**25**
B. lagopus	14	14	10	5	2	2	0	**7**
C. flammea	25	25	25	25	25	25	25	**25**
C. lapponicus	25	24	22	17	19	18	15	**20**
C. temminckii	22	22	20	17	17	16	14	**18**
F. montifringilla	25	25	25	25	25	25	21	**24**
L. lagopus	25	25	25	25	21	4	0	**18**
L. svecica	25	25	25	25	25	25	25	**25**
M. alba	25	25	25	25	25	25	25	**25**
O. oenanthe	25	25	25	25	25	25	25	**25**
P. apricaria	25	25	25	25	25	25	25	**25**
P. trochilus	25	25	25	25	25	25	24	**25**
S. longicaudus	25	25	25	24	24	21	19	**23**
T. iliacus	25	24	25	24	22	20	15	**22**
T. pilaris	25	23	23	22	21	19	16	**21**
Mean	**23**	**23**	**22**	**21**	**21**	**19**	**17**	