Documenting lemming population change in the Arctic: Can we detect trends?

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1   **ABSTRACT**

2   Lemmings are a key component of tundra food webs and changes in their dynamics can

3   affect the whole ecosystem. We present a comprehensive overview of lemming monitoring

4   and research activities, and assess recent trends in lemming abundance across the circumpolar

5   Arctic. Since 2000, lemmings have been monitored at 49 sites of which 38 are still active.

6   The sites were not evenly distributed with notably Russia and high Arctic Canada

7   underrepresented. Abundance was monitored at all sites, but methods and levels of precision

8   varied greatly. Other important attributes such as health, genetic diversity, and potential

9   drivers of population change, were often not monitored. There was no evidence that lemming

10   populations were decreasing in general, although a negative trend was detected for low arctic

11   populations sympatric with voles. To keep the pace of arctic change, we recommend

12   maintaining long-term programs while harmonizing methods, improving spatial coverage and

13   integrating an ecosystem perspective.

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16   **Keywords**

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INTRODUCTION

Lemmings are key herbivores in arctic tundra ecosystems where they play a major role both for the flow of energy from plants to avian and mammalian predators and the dynamics of the vertebrate food web (Gilg et al. 2003; Legagneux et al. 2012). Lemmings can consume more plant material than large herbivores (Batzli et al. 1980) and as prey, they constitute the main resource for many arctic predators (Krebs 2011; Schmidt et al. 2012). Lemmings are also well known for their population cycles with large periodic outbreaks (Stenseth and Ims 1993). These cycles create boom and bust dynamics, which influence the whole vertebrate tundra food web (Ims and Fuglei 2005). The fluctuations of furbearers such as arctic foxes resulting from these resource pulses have been known by hunters and trappers for centuries and eventually lead to the discovery of their persistent regularity – the 3-5-year lemming cycle (Elton 1942). In addition to plants and predators, which interact with lemmings directly, many ground nesting birds, such as geese and waders, are indirectly affected by the lemming cycles as alternative prey for predators (Bêty et al. 2002).

Arctic lemmings belong to two genera, collared lemmings (*Dicrostonyx* ssp.) and brown lemmings (*Lemmus* ssp.), which are represented by six and four geographic species in the Arctic, respectively (CAFF 2013). The two genera of lemmings appear to have co-evolved with the tundra biome since the beginning of the Pleistocene (Oksanen et al. 2008). In this cold environment with long winters, they have developed convergent adaptations to life under the snow, including growing large claws for digging (*Dicrostonyx*, and to a certain extent Norwegian lemmings) and developing robust teeth, strong jaws and large guts enabling them to survive on coarse food plants of low nutritive value. This last adaptation to harsh arctic conditions has been hypothesized to be at the cost of agility to escape predators, making lemmings particularly vulnerable to predation (Oksanen et al. 2008). In the high

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43 Arctic, lemmings are the only naturally occurring small rodent species. *Dicrostonyx* and

44 *Lemmus* often occur together, but there are never more than one species per genus at a given

45 locality. In the low Arctic and in mountain tundra areas further south (Oroarctic, Virtanen et

46 al. 2016; Fig. 1), they usually occur in sympatry with voles (genus *Microtus* and/or *Myodes*),

47 but persist primarily at higher altitudes, where vole densities are low (Ekerholm et al. 2001).

48 The population dynamics of sympatric small rodent species are often synchronous, and both

49 direct and indirect interactions mediated by shared predators have been hypothesized to occur

50 between species (Oksanen 1993; Hanski and Henttonen 1996).

51 As small rodents specialized for life under the snow, lemmings are able to reproduce in

52 winter (Dunaeva 1948; Millar 2001). In high arctic areas where summer predation is intense,

53 the main population growth occurs in winter and density declines over the summer (Gilg

54 2002; Fauteux et al. 2015). Because winter reproduction appears to be a prerequisite for

55 lemmings to reach peak densities, they are likely to be more sensitive to changing winter

56 climate than northern voles (Ims et al. 2011). Unstable autumn and winter weather with warm

57 spells and rain, leading to icing at the bottom of the snow pack, may prevent lemmings from

58 moving in the subnivean space and thus limit their access to food plants (Berteaux et al.

59 2016). In recent decades, a fading out of lemming outbreaks associated with lower

60 abundances has been reported from several regions, notably from high Arctic Greenland

61 (Gilg et al. 2009) and southern Fennoscandia (Kausrud et al. 2008). These changes in

62 dynamics have been attributed to changes in winter climate. In eastern Greenland the collapse

63 of the lemming cycles has had dramatic consequences for specialist predators such as snowy

64 owls (Schmidt et al. 2012). Lemmings are therefore not only a key functional component of

65 the tundra ecosystem, but also a key monitoring target for changes in the arctic tundra biome

66 (Christensen et al. 2013). Detecting and understanding the multifaceted changes arctic

67 ecosystems are experiencing in relation to global change requires well-designed ecosystem-

68   based monitoring systems (CAFF 2013; Ims and Yoccoz 2017). Lemmings and other arctic

69   small rodents have been identified as an important Focal Ecosystem Component in the

70   Circumpolar Biodiversity Monitoring Program (CBMP), and a number of core attributes for

71   their monitoring have been defined (Christensen et al. 2013).

72   Here we present a comprehensive overview of recent lemming monitoring and research

73   activities in the Arctic, including oroarctic areas (Fig. 1). We assess spatial and temporal

74   coverage of current monitoring efforts and the extent to which they address the core attributes

75   for small mammals defined by the CBMP. We discuss the consequences of having gaps in

76   monitoring effort and data availability, and identify ways (and limitations) to

77   harmonize/standardize monitoring protocols. The second aim of this study is to collate the

78   data from these monitoring initiatives in an attempt to assess the status and recent trends of

79   lemming populations across the circumpolar Arctic. We assess geographic patterns in

80   multiannual density fluctuations and examine temporal trends in lemming abundance. In

81   particular we assess whether there is empirical evidence for a circumpolar decrease in

82   lemming populations, which could be hypothesized to result from climate change. We also

83   provide an overview of small rodent community composition.

84   **MATERIALS AND METHODS**

85   **Inventory of lemming monitoring initiatives**

86   For our overview of lemming monitoring, we collected information about recent small rodent

87   monitoring and research activities throughout the Arctic, and south of the Arctic where

88   lemmings are important. Temporally, we included only the programs that have been

89   collecting data after 2000 (Table S1). Contacts were made with relevant scientists from the

90   Small Mammal Expert network of CAFF (https://www.caff.is/terrestrial/terrestrial-expert-

91   networks/small-mammals). Scientists were asked to provide information about their

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92   monitoring/research activities and protocols used, which Focal Ecosystem Component

93   attributes were addressed (abundance, health and phenology are regarded as essential, while

94   demographics, spatial structure and genetic diversity are recommended; Christensen et al.

95   2013), and what other ecosystem components were monitored (Table S2). All scientists were

96   asked to forward the request to other people having relevant data. For Russia, the rodent

97   abundance overview of the International Breeding Conditions Survey on Arctic Birds

98   (http://www.arcticbirds.net/) were also used to identify ongoing projects.

Assessment of status and trends

100   All data custodians were asked to share their data on small rodent abundances or indices to

101   contribute to this circumpolar assessment. As many of the time series were shorter than

102   required for rigorous statistical analyses (spectral or autoregressive analysis), we adopted a

103   graphical approach: Annual time series for each lemming species at each site were plotted to

104   assess population dynamic patterns (variability and cyclicity). To include as many localities

105   as possible, we plotted and analysed data for all sites with at least 5 years of data. When the

106   data consisted of a spring and a fall trapping session each year (Table S1), an average yearly

107   abundance index was calculated, assuming that an average between a spring and a fall session

108   is most comparable to data from a session in the middle of the summer as carried out in amny

109   high Arctic sites. Where present, sympatric voles were also displayed on the plots.

110   The amplitude of multiannual density fluctuations was quantified by the standard deviation of

111   the log-10 transformed annual estimates (s-index; Henttonen et al. 1985). Values of 0 were

112   replaced with half of the smallest value which could have occurred in the series (i.e., half of

113   one animal trapped or half of one nest found; Gruyer et al. 2008). In some sites, notably in

114   Fennoscandia, lemmings appeared sporadically and were only registered in some years.

115   Therefore, we also quantified the irregularity of lemming presence in each series as the

116   overall proportion of years where trapping was carried out but no lemmings were caught.

117   For sites where both lemmings and voles occurred, average community composition was

118   characterized by calculating the mean of the annual proportions of lemmings (both species

119   together where two species were present) across all years. Similarly, the mean of the annual

120   proportions of each species of lemmings was calculated relative to the total abundance of

121   lemmings for sites where two species of lemmings occurred.

122   Trends of lemming abundance were assessed as the slope of a linear regression of abundance

123   estimates against time. Abundance estimates were scaled to a mean of 0 and a standard

124   deviation of 1. For the trend analysis, we used only time series with observations over at least

125   10 years. Moreover, we focused on data from the last 25 years (1993–2017) to compare

126   trends over a specific time period. We tested for differences in the estimated trends (i.e. slope

127   coefficients) among bioclimatic zones, species, geographical regions and sites with different

128   community composition. For this analysis, the trends were used as response variable in linear

129   models with the respective categories as explanatory factors. To account for different lengths

130   of the time series, length was included as a weighting parameter. Results for the different

131   categories are presented as predicted means with 95% confidence intervals. For sites where

132   lemmings co-occurred with voles, we also estimated linear trends in the annual proportion of

133   lemmings (both *Lemmus* and *Dicrostonyx* if two lemming species were present) in the total

134   abundance of rodents, and, where two lemming species were present, in the annual proportion

135   of *Dicrostonyx* relative to total lemming abundance. All statistical analyses were carried out

136   in R version 3.5.0 (R Development Core Team 2018).

137   **RESULTS**

138   **Inventory of monitoring projects**

139 We obtained information from 49 sites, where lemmings were monitored after the year 2000

140 (Fig. 1, Table S1). The sites belong to all geographic regions of the Arctic: 15 in North

141 America, three in Greenland, 21 in Fennoscandia including the Kola Peninsula (hereafter

142 referred to as Fennoscandia), and 10 in Russia east of the White Sea (hereafter referred to as

143 Russia). Fennoscandia is thus clearly overrepresented relative to the geographical area it

144 covers, whereas Russia is underrepresented. Considering only ongoing monitoring initiatives

145 (78 %), the geographic skew is even stronger with six ongoing programs in Russia, 18 in

146 Fennoscandia, three in Greenland and 12 in North America. The biased geographical

147 coverage resulted also in a biased species coverage with an over-representation of the

148 Norwegian lemming. Regarding bioclimatic zones (Fig. 1), 12 sites are located in the high

149 Arctic, 16 sites in the low Arctic, and 21 sites in the Oroarctic.

150 Temporally, the monitoring activities extended over periods ranging between 3 and 87 years

151 (Fig. 2, Table S1). In eight sites, observations were lacking for some years. A majority of the

152 ongoing monitoring activities started in the beginning of the 1990s or later, and only one

153 program in each of North America and Greenland, five in Fennoscandia and three in Russia

154 began prior to 1990. There were, however, other monitoring programs taking place in the 20th

155 century, which are not included here as they stopped before 2000 (Kokorev and Kuksov

156 2002; Krebs et al. 2002; Pitelka and Batzli 2007).

157 Among the essential monitoring attributes of the CBMP, annual lemming abundance (mostly

158 indices) were recorded at all sites (Fig. 3). The methodologies varied between sites and

159 include snap-trapping, live-trapping, winter nest counts, systematically recorded incidental

160 observations, and qualitative indices (Fig. 4). Snap trapping was the most used method

161 overall, and live-trapping was mostly used in North America. Qualitative indices based on a

162 general impression of lemming abundance in the field were used at least partly in half of the

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163   Russian sites. Among these methods, only live trapping allows the estimation of true

164   densities and all other methods provide relative abundance indices. At many sites (69%)

165   several monitoring methods were used (Table S2).

166   The two other essential attributes of the CBMP plan received limited attention. Health

167   parameters (diseases, parasites) were only monitored systematically at a few sites. Phenology

168   was regularly monitored only on Wrangel Island, where dates of first appearances on the

169   snow, migration to summer habitat and observations of first juveniles were recorded (Fig. 3,

170   Table S2). Of the recommended attributes, about half of the sites monitored some aspects of

171   lemming demography and spatial structure regularly. Sex, age classes and sometimes

172   reproductive status of trapped animals were recorded, but mortality was rarely determined.

173   As trapping was often carried out in a design of replicated plots in different habitats, the data

174   also provided some information about spatial structure (habitat use). Similar information can

175   be obtained from winter nest counts. Genetic diversity was surveyed in some sites, but often

176   only once (Fig. 3, Table S2). In addition to these attributes, a few programs examined

177   lemming diets (Table S2). Regarding other ecosystem parameters, the abundance and

178   reproduction of lemming predators, as well as the availability of alternative prey for the

179   predators was monitored at about half of the sites, but plant productivity and phenology

180   received less attention (but see Björkmann et al. 2020). Finally, less than half of the sites

181   monitored abiotic conditions annually (Table S2). The size of the study area (Table S1) and

182   the total effort used in monitoring (e.g. total number of trap nights per session) also varied

183   considerably between sites.

184   **Status of lemming populations**

185   Through our common effort and willingness to share data, we were able to assemble

186   abundance time series for 43 sites (Fig. 1, Fig. S1), including 14 time series for *Dicrostonyx*,

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187   18 for *Lemmus lemmus*, eight for other *Lemmus* species and nine for the combined abundance

188   of *Dicrostonyx* and *Lemmus* (length ≥ 5 years). In addition, abundance indices for voles were

189   recorded at 27 sites (63% of the sites; table S1). Small rodent communities were composed of

190   both voles and lemmings at all sites south of the high Arctic, except Walker Bay (Fig. 1). In

191   Fennoscandia, voles were on average more abundant than lemmings in trapping data, whereas

192   in North America several mixed communities occurred where lemmings were more abundant

193   than voles (Fig. 1).

194   The available data present a very heterogeneous picture of temporal dynamics (Fig. 1, Fig.

195   S1). Considerable multiannual fluctuations in abundance were recorded at all sites and for

196   most species, but patterns of fluctuations differed considerably. Norwegian lemmings

197   exhibited typical outbreak years at intervals of three to six years, but sometimes much longer

198   periods occurred without outbreaks or even without lemming records at all (Fig. 1B). Vole

199   peaks in Fennoscandia were often synchronous with lemming peaks, but sometimes vole

200   peaks occurred without lemmings. Outside of Fennoscandia, heterogeneity in population

201   dynamics was also large (Fig. 1A). Rather regular cycles with a period of 3–4 years were

202   observed at some sites such as Bylot Island, but this pattern was not the general rule. Other

203   sites exhibited multiannual fluctuations with a period of 4 or 5 years, but patterns were much

204   less apparent because of large differences in abundance indices between different peak years

205   (e.g. Utqiaġvik, Aulavik).

206   Amplitude, as estimated by the s-index, ranged from 0.26 to 0.91 (Table S3). The s-index was

207   below the threshold defined for high amplitude population fluctuations (0.5; cf. Henttonen et

208   al. 1985) in 11 time series (26%) and in most of these, lemmings occurred only rarely or at

209   very low abundances (Kilpisjärvi, Daring Lake). On average, amplitude estimates were

210   highest for Norwegian lemmings (Fig. 5). The observation method that recorded the highest

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211   amplitudes was incidental observations. Series based on winter nests and live trapping

212   exhibited high variation in s-index. The proportion of years with zero lemmings trapped had a

213   lower median for *Dicrostonyx* than for the other species, but there were large differences

214   among study sites, and between trapping methods (Fig. 5). Snap trapping data had more zero

215   observations than any other methods.

216   Comparing lemming abundance between sites is difficult because of the various methods

217   used. Indeed, statistically derived density estimates based on live trapping were available

218   only for four high Arctic sites (Fig. 1, Fig. S1). Snap trapping indices show large differences

219   in the number of lemmings trapped in peak years with captures of up to 15 (Joatka) and even

220   30 (Finse) individuals per 100 trap-nights in Fennoscandia, whereas at some other sites

221   captures were less than 1 capture per 100 trap-nights in all years (Daring Lake). In addition to

222   differences in densities between areas and species, these differences were likely related to

223   differences in trapping design among studies (Fauteux et al. 2018), and possibly to

224   differences in trapability of the different species.

225   **Trends**

226   Linear trends for scaled lemming abundance over the last 25 years (42 series, mean length

227   19.1 years) varied between -0.87 (Chaun) and 0.82 (East Bay) standard deviations per decade

228   (Table S3). The mean trend was -0.011 (SD = 0.051), yielding no evidence of a panarctic

229   increasing or decreasing trend for lemming populations over the last 25 years. There were no

230   consistent differences in trends between species or bioclimatic zones, although estimates for

231   the low Arctic were slightly negative (Fig. 6). Concerning geographical regions, there was an

232   indication for a negative trend in Russia. For community composition, trends were on

233   average not different from 0 for sites where only lemmings are present and for Fennoscandian

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234   sites with Norwegian lemmings and voles, but they were significantly negative for sites

235   where arctic lemmings and voles co-occur (Fig. 6).

236   Trends in the proportion of lemmings compared to voles and in the proportion of each species

237   among lemmings were mostly weak and not significant (Table S3). A change in species

238   composition was, however, recorded at two low Arctic sites. In Churchill, Manitoba, no voles

239   had been trapped in the 1990's, but when trapping was resumed in 2010, meadow voles

240   (*Microtus pennsylvanicus*) were caught. Similarly, *M. middendorffii* voles were observed in

241   South-eastern Taimyr in 2013 and 2014 for the first time despite years of monitoring earlier

242   (Golovnyuk 2017).

243   **DISCUSSION**

244   **Monitoring**

245   The present inventory revealed a considerable effort to investigate and monitor lemming

246   populations in the circumpolar Arctic. Monitoring/research initiatives are ongoing at 38 sites

247   covering most regions of the Arctic, and in many sites data are available for 20 years or more.

248   While in some programs lemmings are the focus of specific research questions (Finse,

249   Walker Bay), at other sites small rodent abundance is mostly surveyed to explain variation in

250   other ecosystem components, such as breeding birds (south-eastern Taimyr, Karrak Lake),

251   specialist predators (Børgefjell II, Helags) or vegetation dynamics (Joatka, Abisko). The

252   objectives likely influence the choice of methods, temporal and spatial sampling design and

253   resources allocated to this task. This fact, together with the inherent challenges of long-term

254   fieldwork in remote arctic locations, may explain why methods used to monitor lemming

255   abundance vary so much. Despite a substantial overall effort, biases in geographic

256   distribution of sites and several short time series, some of them with gaps, limit the reliability

257   of a general assessment of status and long-term trends of lemming populations in the Arctic.

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258   The geographical distribution of monitoring sites is far from uniform (Fig. 1). Numerous sites

259   in Scandinavia, where access is relatively easy by arctic standards and researcher density is

260   high, lead to a good coverage for the Norwegian lemming, but less so for other more

261   widespread species. In the Russian Arctic, there are only four ongoing monitoring initiatives

262   with more than five years of data. The lack of data from Russia not only regarding lemmings,

263   but for many important ecosystem components, has been highlighted in previous assessments

264   (CAFF 2013) and hampers a circumpolar understanding of changes in the tundra ecosystems.

265   Monitoring in the Canadian Arctic Archipelago is also sparse, mostly due to remoteness.

266   Another gap in spatial coverage is south of the Arctic proper outside of Fennoscandia (Fig.

267   1), despite distributions of several lemming species extending into these areas (Stenseth and

268   Ims 1993). This limits our ability to detect possible range shifts (Marcot et al. 2015).

269   Many of the longer series go back to the beginning of the 1990s, which represents 25 years or

270   more of fieldwork, a substantial effort. However, this is also a period during which mean

271   temperature in the Arctic increased consistently (Overland et al. 2015). Thus, the data do not

272   allow a direct comparison to the period before recent Arctic warming occurred. In this paper

273   we focussed on ongoing monitoring and excluded data from older research programs

274   completed before 2000. Assessments of changes in lemming dynamics covering longer

275   periods have, however, been published for specific regions and suggest a substantial amount

276   of non-stationary dynamics (Angerbjörn et al. 2001; Aharon-Rotman et al. 2015).

277   Seasonally, lemming monitoring is usually carried out during one or two periods in summer.

278   Analysing trends for specific seasons (spring or fall) may reveal changes important for

279   trophic interactions (Ims and Fuglei 2005), but could not be done here because many data

280   series consisted of one estimate per year. There are virtually no data on lemming abundance

281   or activity during the long winter period, apart from counts of winter nests after snowmelt,

282   although winter is likely to be critical to understand population dynamics (Krebs 2011;

283   Domine et al. 2018) and the impact of climate change (Kausrud et al. 2008) in animals

284   specialized for life under the snow. This knowledge gap has been stressed for a while

285   (Stenseth and Ims 1993), but the challenges of studying lemmings under the snow in remote

286   arctic locations are difficult to overcome. However, new technology is about to open up new

287   possibilities through the development of camera tunnels for monitoring lemmings year-round,

288   providing information about presence and timing of reproduction (Soininen et al. 2015).

289   Population density is a crucial parameter in ecology, but it is often difficult to estimate

290   reliably. Most methods used to monitor lemmings provide abundance indices. Real density

291   estimates are obtained only from live trapping and subsequent mark-recapture analyses,

292   which is a labour-intensive method usually carried out with a rather limited spatial extent.

293   Several sites in North America moved from snap trapping to live trapping during the

294   monitoring period (e.g. Bylot), improving data quality and providing additional information

295   on vital rates such as survival. A recent study assessing how well different abundance indices

296   are correlated with true density estimates concluded that systematic incidental observations

297   and snap trapping provided equally good proxies for lemmings in the high Arctic (Fauteux et

298   al. 2018). Incidental observations are easy to implement, but they usually do not distinguish

299   between species. Moreover, it is unclear whether they would work as well in the low Arctic

300   where lush vegetation may hamper detection. Snap trapping is the most commonly used

301   method, but the sampling design used in Fennoscandia often does not target lemming habitat

302   specifically, which results in series with many zero values and subsequent analytical

303   challenges (Fig. 1).

304   The variety of methods used is a challenge when inferring large scale patterns (Berteaux et al.

305   2017). While all quantitative methods allow comparisons of trends and relative dynamic

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306   patterns, it can be difficult to compare abundance among sites, which may be the most

307   important parameter to predict for instance trophic interactions (Henden et al. 2010).

308   Moreover, the large heterogeneity in dynamics seen on Figures 1 and S1 may be partly due

309   differences in methods. For instance, incidental observation and winter nests series have

310   considerably less 0-values than snap trapping series, and qualitative index series tend to have

311   more regular cycles than quantitative series. For long qualitative time series, there can also be

312   an effect of shifting base-line when assessing abundance, making it difficult to infer long-

313   term trends. Such considerations argue in favour of the standardization of monitoring

314   methods across sites. However, adoption of new protocols in a long-term program is

315   challenging. Old and new protocols should be run simultaneously for a number of years to

316   establish correction factors between time series. This may be difficult to implement

317   logistically, but can result in well-assembled long time series, such as in Bylot or Karupelv

318   (Gilg et al. 2006; Gauthier et al. 2013).

319   Parasites and diseases of lemmings, two indicators of health, have been studied at a few sites

320   (Table S2), but are usually not included in regular monitoring protocols. This may be due to

321   the tendency to study parasites separately from food web oriented ecosystem research

322   (Lafferty et al. 2008), the latter of which most lemming monitoring programs belong to.

323   Genetic diversity is also usually addressed in snapshot studies looking at population structure

324   or phylogeography (Ehrich et al. 2001), but is not investigated regularly. Tissue samples

325   collected either occasionally or systematically from trapped animals could, however, be used

326   for retrospective analyses of genetic structure or diseases/parasites. Phenology, in particular

327   the timing of winter reproduction, is an important parameter to understand how changes in

328   winter climate may be affecting lemming population dynamics. Unfortunately, present

329   monitoring methods such as discrete trapping sessions or winter nest counts do not provide

330   this information.

14

331 An ecosystem-based approach to monitoring, structured around explicit models for

332 interactions between ecosystem components and drivers of change, is recommended by the

333 CBMP (Christensen et al. 2013), and applied in some of the initiatives providing lemming

334 data (e.g, Varanger, Zackenberg; Ims and Yoccoz 2017; Schmidt et al. 2017). Analysing

335 trends of change as functions of ecological drivers is only possible if likely drivers of change

336 are also measured at a relevant scale. To address how abiotic and biotic drivers influence

337 lemming population dynamics and other lemming attributes, monitoring/research projects

338 should take an ecosystem-based approach and collect data about a selection of other

339 important state variables (Ims and Yoccoz 2017). Addressing the hypothesized importance of

340 snow conditions for lemmings requires for instance some local data about snow such as snow

341 physical properties, snow cover duration or depth (Domine et al. 2018). Remote sensing data

342 and snow modelling can also provide useful information.

343 **Status and trends**

344 The large heterogeneity in patterns of lemming dynamics observed here is in accordance with

345 previous work. The amplitude of lemming fluctuations often varies (CAFF 2013) and

346 dynamics in some areas can look more like irregular outbreaks than typical population cycles

347 (Ims et al. 2011). The longer series, at least for Norwegian lemmings, suggest non-stationary

348 dynamics characterized by periods with regular cycles followed by periods with persistent

349 low density over a decade or more (Finse, Joatka and Laplandsky, Fig. 1). Similar patterns

350 have been documented over the last century based on diverse sources of evidence

351 (Angerbjörn et al. 2001). This natural variability in lemming dynamics makes population

352 trends inherently difficult to detect, in particular considering the modest length of most time

353 series (McCain et al. 2016). This implies that our result of no overall trend in lemming

354 populations across the circumpolar region needs to be considered cautiously. The exception

355 are abrupt changes in dynamics such as in NE Greenland (Karupelv and Zackenberg; Gilg et

356 al. 2009) or at Finse, where the disappearance of cycles in the late 1990s may be attributed to

357 changes snow conditions (Kausrud et al. 2008). At Finse, however, a new outbreak occurred

358 in 2014 (Fig. 1), indicating that also the more recent changes may be transient.

359 Regionally, our results indicate that lemming populations co-occurring with one or several

360 species of voles outside Fennoscandia may be declining. This finding is in agreement with a

361 predicted decline of specialized arctic species at the southern edge of their distribution

362 (Loarie et al. 2009). At the same time, voles have recently appeared in two sites (Churchill

363 and Southeastern Taimyr) indicating a northward advance of these boreal species. It has been

364 hypothesized that Norwegian lemmings at low altitudes may be exposed to apparent

365 competition from voles mediated by shared predators (Oksanen 1993). It is possible that a

366 similar mechanism, together with an increase of generalist predators from adjacent boreal

367 areas (Reid et al. 1995), contributed to the observed declines in lemming populations at these

368 sites. In addition, climate change may lead to more frequent melt and freeze events in winter,

369 which have been hypothesized to be detrimental to the subniveal life of lemmings (Kausrud

370 et al. 2008; Ims et al. 2011; Berteaux et al. 2016). A climate-driven increased growth of

371 meadows and tall shrubs (Myers-Smith et al. 2011) at the detriment of more typical moss-

372 graminoid and dwarf shrub tundra, which is the preferred habitat of lemmings, may also

373 contribute to vole expansion and lemming population decline.

374 The primarily oroartic populations of the Norwegian lemming did not show a similar

375 negative trend, although they always occur together with several species of voles. This could

376 be because they live in mountainous areas, where they have the possibility to exploit

377 altitudinal gradients in winter temperature, snow conditions and productivity (Oksanen 1993;

378 Ims et al. 2011). Moreover, several of the monitored populations were characterized by a

379 large proportion of years without lemming captures, which may indicate that they are not in

380 optimal lemming habitats, but in areas which lemmings colonize only in some peak years.

381 Their permanent habitats might be at higher altitudes (Kalela et al. 1971), where harsh

382 winters provide good snow cover and scarce vegetation prevent voles from establishing.

CONCLUSIONS AND RECOMMENDATIONS

384 Overall, the available time series for lemmings in the Arctic did not show any consistent

385 declining trend. Hence, although low precision of the data need to be kept in mind, our results

386 do not support the contention that climate change has negatively affected lemmings at a

387 global scale so far. However, given the large geographical variability in climate, snow

388 physical properties and community composition across the circumpolar Arctic, this may not

389 be surprising. Nonetheless, when the data were split according to different bioclimatic and

390 community contexts, negative trends were detected in low-arctic populations co-occurring

391 with one or several species of voles. Voles also appeared for the first time in some of these

392 areas during our study period, possibly connected to climate change in accordance with

393 predictions of a northward displacement of arctic specialist species.

394 Considering the important environmental changes that will affect the Arctic in the near future

395 and the critical importance of lemmings in the tundra food web, it is very important to

396 continue and improve monitoring of this group. Based on the present review, we recommend

397 harmonizing as far as possible the collection of abundance data across sites using well

398 described quantitative methods and explicit spatial designs to obtain reliable estimates

399 allowing comparison of patterns among sites. While the continuation of existing time series is

400 a first priority, improving the spatial coverage of monitoring in underrepresented areas such

401 as Russia and the Canadian Arctic Archipelago would be highly desirable. Considering that

402 standardized incidental observationsprovide a comparable measure of abundance and can be

17

403 easily implemented, this simple non-invasive method is recommended for sites with little

404 resources, at least in areas where only lemmings are present. To monitor species-rich low

405 arctic communities, live and snap trapping should be used when possible. The development

406 of new non-invasive methods such as camera tunnels, which have the potential to provide

407 year-round information, should also be continued. In addition to abundance, the collection of

408 data on potential drivers of change and on other attributes recommended by CBMP such as

409 parasites/diseases and phenology should be improved.

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A.

High Arctic
Low Arctic
Subarctic
Oroarctic

▲ *Lemmus* only
◆ *Dicrostonyx* only
⬟ 2 species, *Dicrostonyx* more abundant
■ 2 species, *Lemmus* more abundant
▨ Lemmings with voles in minority
☐ Lemmings with voles in majority
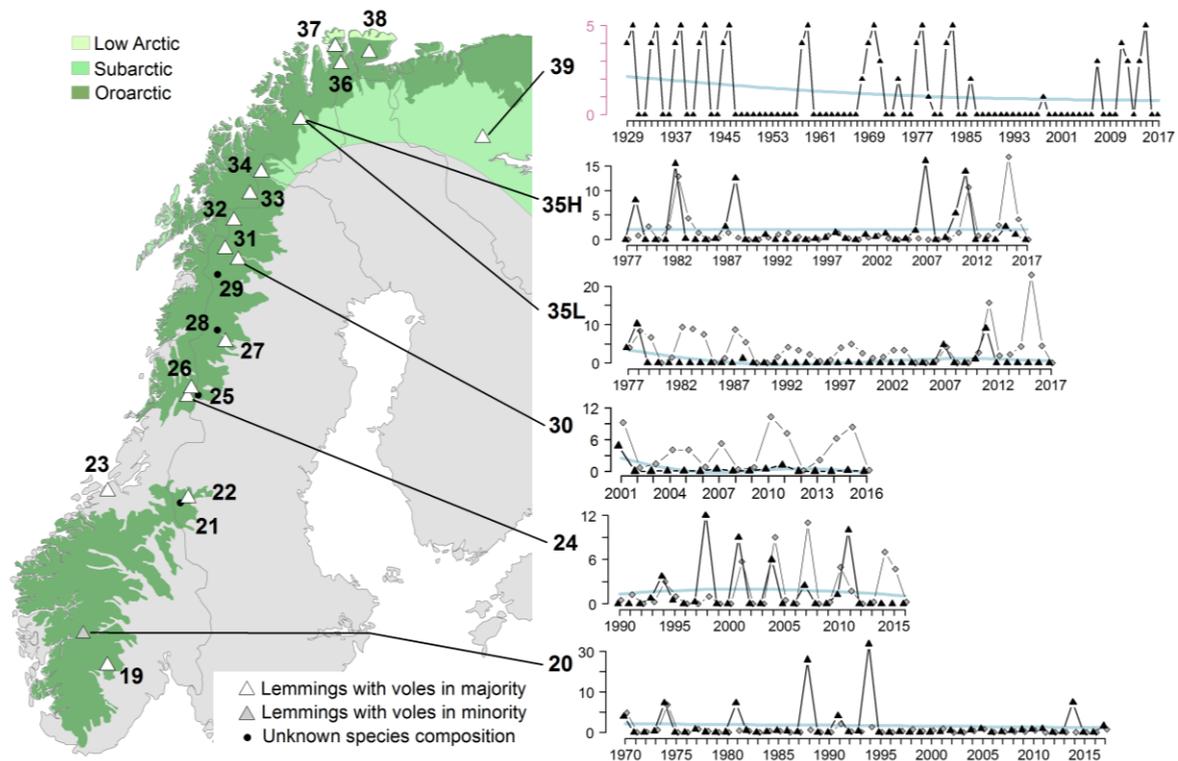• Unknown species composition

B.

Figure 1. Maps showing the locations of lemming monitoring sites in A. Circumpolar region and B. Fennoscandia (delimited by the large grey square in panel A). Different shadings of green indicate the delimitations of bioclimatic subzones. The high Arctic, low Arctic and Subarctic are drawn according to CAFF (2013) and the Oroarctic, which is customarily pooled with the arctic tundra in global biome overviews and represents potential habitat for lemmings south of the Arctic proper, according to Virtanen et al. (2016). Numbers refer to the sites as listed in Table 1 and symbols indicate small rodent community composition. Time series of annual small rodent abundance estimates are presented for selected sites (graphs for the remaining sites are given in Fig S1). On the time series graphs, triangles represent lemmings (upwards and black for *Lemmus*, and downwards and white for *Dicrostonyx*), circles represent data not identified to species such as winter nests, qualitative indices or incidental observations, whereas grey squares represent voles (all species pooled). The colour of the y-axis indicates the data type: black refers to individuals caught per 100 trap nights (6, 8, 41 and all Fennoscandia except 39), light blue to density in individuals per ha (13, 16, 17), green to winter nest density in nests per ha (11), orange to incidental observations (numbers seen per observer-day [1], or observer-hour [15]) and purple to qualitative indices (39, 44, 48, 49). Smoothed trend lines for the total abundance of lemmings are shown in light blue. 35H and 35 L refer to the highland and lowland series of Joatka (Table S3).
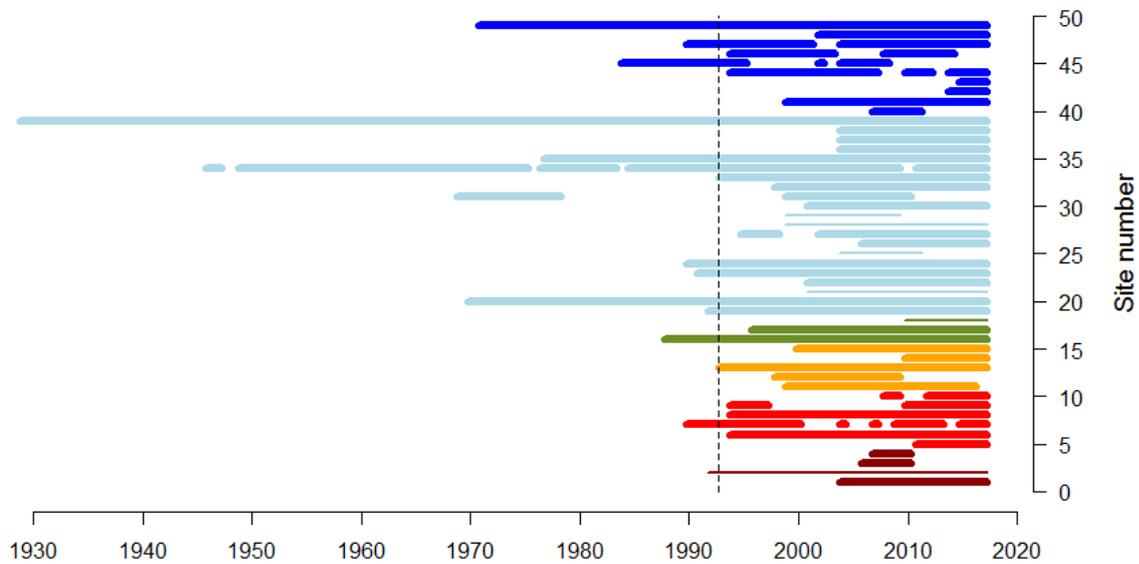
23

Figure 2. Extent of time during which lemmings have been monitored in the Arctic. Only sites which have still been collecting data after 2000 were included in this study. Sites are ordered according to site numbers listed in Table 1 and mapped in Fig. 1. Colours refer to geographic regions: brown — North America west of the Mackenzie River; red — mainland North America east of the Mackenzie River; orange — Canadian Arctic Archipelago; green — Greenland; light blue — Fennoscandia including the Kola Peninsula; blue — Russia east of the White Sea. Thick lines indicate sites from which data were included in the status and trends analysis, whereas thin lines refer to sites from which raw data were not contributed. The dotted vertical line shows 1993 and highlights the start of the last 25 years, which is the period for which trends were calculated.
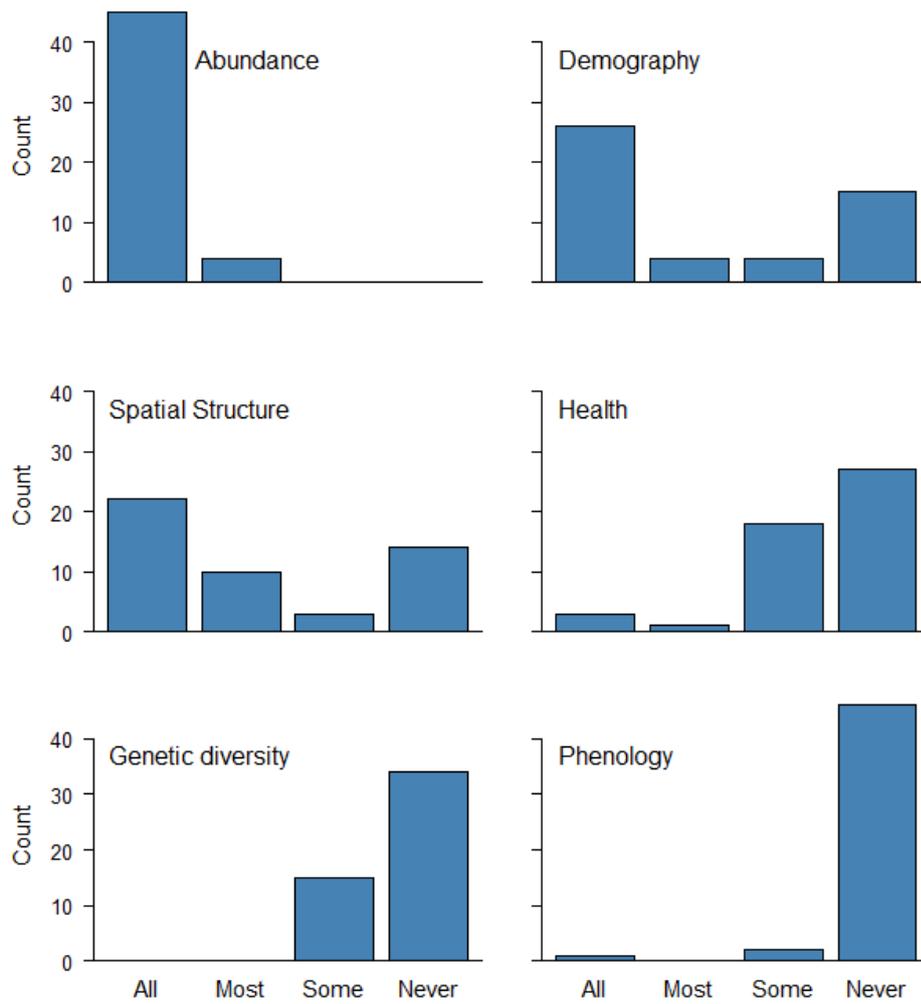
24

Figure 3. Number of sites where the core attributes defined by CBMP for small mammals were monitored according to the frequency of data collection: data collected during "All", "Most", or "Some" years, or "Never" (compiled from Table S2).
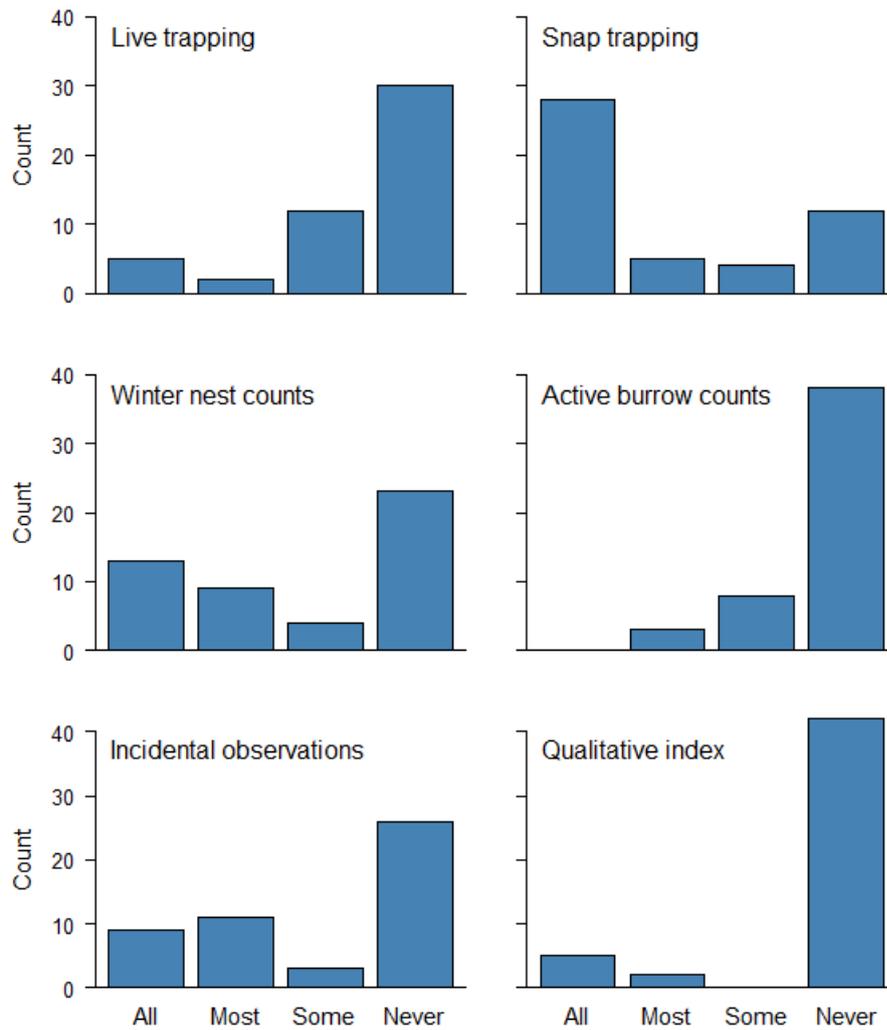
Figure 4. Methods used to assess lemming abundance. For each method the number of sites where it was used is plotted according to the frequency of data collection: data collected during "All", "Most", or "Some" years, or "Never" (compiled from Table S2). Qualitative indices are integer index values based on a general impression of lemming abundance in the field, sometimes explicitly related to the number of lemmings seen per day.
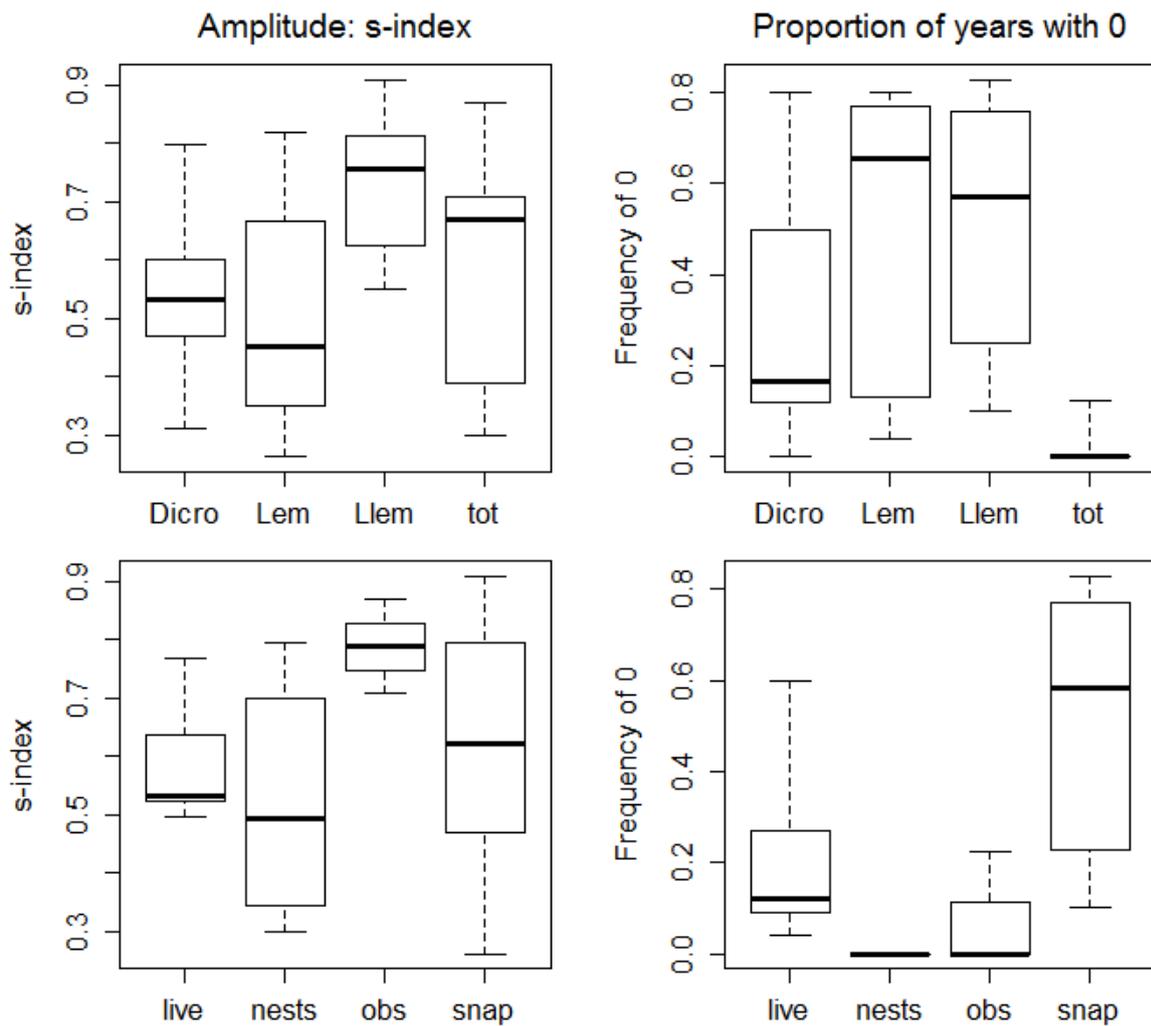
Figure 5. Boxplots of s-index values (see methods) and the proportion of years with abundance estimates of 0 according to species (Dicro = *Dicrostonyx* spp.; Lem = *Lemmus* spp. except *L. lemmus*; Llem = *L. lemmus* and tot = two lemming species together) and to observation method (live = live trapping; nests = winter nest counts; obs = incidental observations; snap = snap trapping). Boxes represent the middle 50% of the data with the median (thick line). Whiskers extend to the extreme values.
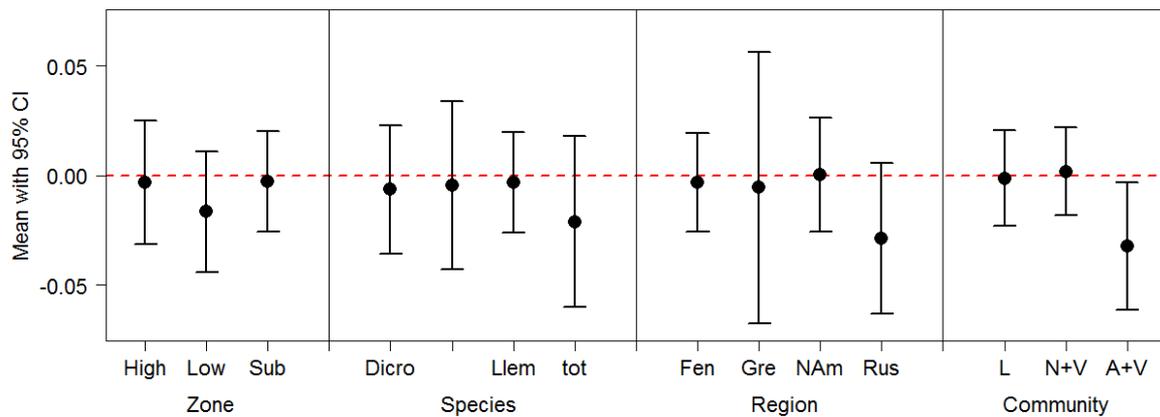
Figure 6. Predicted mean linear slopes of lemming abundance as estimated from linear models with 95% confidence intervals for time series scaled to 0 mean and standard deviation of 1. The y-axis is in units of standard deviation per year. Linear trends were analysed with respect to bioclimatic zone (High Arctic, Low Arctic and Oroarctic), species (Dicro = *Dicrostonyx* spp.; Lem = *Lemmus* spp. except *L. lemmus*; Llem = *L. lemmus* and tot = two lemming species together), geographic region (Fen = Fennoscandia; Gre = Greenland; NAm = North-America; Rus = Russia east of the White Sea), and the community composition at each site (L = only one or two species of lemmings; N+V = *L. lemmus* and several species of voles; A+V = arctic lemmings (all species except the Norwegian lemming) and one or several species of voles; see table S1 for voles species at each site). Numbers above the x-axis indicate the number of time series in each category.

28

Table 1. List of lemming monitoring sites with the site number, site name, region and country indicated. See Figure 2 for duration each site was monitored.

Site number and name	Region and country
1. Utqiaġvik (Barrow)	Alaska, USA
2. Utqiaġvik (Barrow II)	Alaska, USA
3. Komakuk	Yukon, Canada
4. Herschel Island	Yukon, Canada
5. Tuktuk	North-western Territories, Canada
6. Daring Lake	North-western Territories, Canada
7. Walker Bay	Nunavut, Canada
8. Karrak Lake	Nunavut, Canada
9. Churchill	Manitoba, Canada
10. Rankin Inlet	Nunavut, Canada
11. Aulavik	North-western Territories, Canada
12. Alert	Nunavut, Canada
13. Bylot Island	Nunavut, Canada
14. Igloolik	Nunavut, Canada
15. East Bay	Nunavut, Canada
16. Karupelv Valley	Greenland
17. Zackenberg	Greenland
18. Hochstetter Forland	Greenland
19. Møsvatn	Telemark, Norway
20. Finse	Hordaland, Norway
21. Helags	Jämtland, Sweden
22. Vålådalen-Ljungdalen	Jämtland, Sweden
23. Åmotsdalen	Trøndelag, Norway
24. Børgefjell TOV	Trøndelag, Norway
25. Borgafjäll	Västerbotten, Sweden
26. Børgefjell	Nordland, Norway
27. Ammarnäs	Västerbotten, Sweden
28. Vindelfjällen	Västerbotten, Sweden
29. Padjelanta	Norrbotten, Sweden
30. Stora Sjøfallet	Norrbotten, Sweden
31. Sitas	Norrbotten, Sweden
32. Abisko	Norrbotten, Sweden
33. Dividalen	Troms, Norway
34. Kilpisjärvi	Lapland, Finland
35. Joatka	Finnmark, Norway
36. Ifjord	Finnmark, Norway
37. Nordkyn Peninsula	Finnmark, Norway
38. Varanger Peninsula	Finnmark, Norway
39. Laplandskiy Zapovednik	Murmansk Obl., Russia
40. Nenetskiy	Nenetskiy AO, Russia
41. Erkuta	Yamal, Russia
42. Sabetta	Yamal, Russia
43. Belyi Island	Yamal, Russia
44. Meduza Bay	Taimyr, Russia
45. Mys Vostochnyi	Taimyr, Russia
46. South-eastern Taimyr	Taimyr, Russia
47. Jukarskoe	Yakutia, Russia
48. Chaun	Chukotka, Russia
49. Wrangel Island	Chukotka, Russia