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Taking the beat of the Arctic: are lemming population cycles changing due to winter climate?

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Reports of fading vole and lemming population cycles and persisting low populations in some parts of the Arctic have raised concerns about the spread of these fundamental changes to tundra food web dynamics. By compiling 24 unique time series of lemming population fluctuations across the circumpolar region, we show that virtually all populations displayed alternating periods of cyclic/non-cyclic fluctuations over the past four decades. Cyclic patterns were detected 55% of the time ($n = 649$ years pooled across sites) with a median periodicity of 3.7 years, and non-cyclic periods were not more frequent in recent years. Overall, there was an indication for a negative effect of warm spells occurring during the snow onset

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period of the preceding year on lemming abundance. However, winter duration or early winter climatic conditions did not differ on average between cyclic and non-cyclic periods. Analysis of the time series shows that there is presently no Arctic-wide collapse of lemming cycles, even though cycles have been sporadic at most sites during the last decades. Although non-stationary dynamics appears a common feature of lemming populations also in the past, continued warming in early winter may decrease the frequency of periodic irruptions with negative consequences for tundra ecosystems.

1. Introduction

Small mammals play a key role in terrestrial ecosystems through numerous linkages with their forage plants and predators [1–3]. In species-poor systems, such as boreal, Arctic and alpine ecosystems, fluctuations in small mammal populations can regulate trophic dynamics of a significant part of the ecosystem and are crucial to maintain biodiversity of the predator guild and of plant communities [3–6]. Warming climate at high latitudes has a strong potential to disrupt these trophic dynamics especially through changes in snow conditions [7,8]. For instance, changing snow depth can alter predation rate of snowshoe hares (*Lepus americanus*) and disrupt the cyclic dynamics of this food web [9].

Lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) are the most common small rodents of the Arctic tundra and are well known for their large population fluctuations, typically with 3- to 5-year periodicities [10,11]. Their population fluctuations have become classic textbook examples of animal population cycles, the causes of which having generated intense debates (see e.g. [11,12]), although an emerging consensus points toward delayed density dependence governed by trophic interactions [13,14]. Cyclicity of lemming populations, however, appears more variable than generally believed as some populations have been found to be non-cyclic or with irregular fluctuations [5,15,16]. In recent decades, major changes in the dynamics of small mammal populations have been reported in northern Europe [1,17], and lemming populations that were previously described as being cyclic have dampened to no or very weak cycles in Greenland and Fennoscandia [18,19], a phenomenon coinciding with climate warming. Despite limited empirical evidence at large spatial scale, fading lemming cycles due to warmer winters, with dramatic consequences for charismatic predators and the functioning of the food web, have been used as a prime example of climate change impacts on the Arctic wildlife [20].

Lemmings are adapted to the harsh Arctic climate and can breed during the long winters under the snow [21]. Most periodic lemming irruptions depend on high breeding activity in winter [22], and there is evidence that changing snow conditions may be linked to the collapse of lemming and vole populations at certain sites [18,19,23]. During winter, lemmings live in the soft depth hoar that typically forms at the base of the snowpack under a layer of dense, wind-compacted snow [24]. A hardened basal snow layer due to melt–freeze cycles or rain-on-snow events in early winter reduces thermal insulation, may increase the cost of locomotion and limits access to subnivean food plants throughout the snow season for lemmings [25]. The period of snow onset in early winter is especially critical as it may largely determine the thickness, density and hardness of the depth hoar layer for the rest of the winter [8,26]. Reduced duration of snow cover could also be detrimental to lemmings by shortening how long snow offers protection from predators [19,27]. Rapidly increasing temperatures in the Arctic [28,29] can profoundly change physical properties and duration of the snowpack, thereby negatively affecting lemming populations [8,30].

We present the largest circumpolar analysis of lemming populations ever conducted based on 24 time series from 20 high-latitude sites (figure 1; electronic supplementary material, table S1) where we examine recent changes in their population dynamics. Lemming time series were carefully selected from Ehrich *et al.* [32] to retain only high-quality datasets among those available across the Arctic region and the Fennoscandian oroarctic mountain areas (see electronic supplementary material, Material and methods). We first determined the prevalence of lemming population cycles across the circumarctic, their dominant periodicity and the temporal stability of cyclic fluctuations. We further examined whether climatic conditions during winter could be important environmental drivers of change in lemming population dynamics across the circumarctic region, as documented at the local scale [18,19]. We tested two specific hypotheses related to winter climatic conditions. First, warm temperature during the period of snow onset and shortly after should promote melt–freeze and rain-on-snow events, which will lead to a hard basal layer in the snowpack [33,34]. We hypothesized that a hardened snowpack caused by these early winter events should reduce access to subnivean food and impede lemming reproduction, thereby limiting population growth and reducing their abundance (early winter climate hypothesis [8]). Second, shorter winters should limit population growth and densities the following summer by reducing the duration of subnivean reproduction and the period that snow cover protects lemmings from several predators (winter duration hypothesis [19]).

2. Material and methods

(a) Lemming data

The lemming data used in this study were a subset of the population time series assembled from 49 sites across the circumarctic by Ehrich *et al.* [32]. We extracted from this dataset the 24 time series (from 20 sites; some sites had data for two different lemming species) that met the following criteria: (i) they were at least 20 years in length, (ii) data were collected each year during the period 2001–2019, (iii) they had a continuous annual record without any gap (in two cases data were missing for 1 year: Aulavik in 2017 and Åmotsdalen in 2018) and (iv) they used a consistent sampling method with adequate sampling effort throughout the study period. We excluded one series from southern Sweden (Vålådalen/Ljungdalen) where the lemming index was always very low except for 1 year (2011). The criteria applied to select the 24 lemming time series ensured that we had the datasets of highest quality for our analyses among those compiled by Ehrich *et al.* [32] and available for this key group of species across the circumpolar tundra areas. The time series that we retained used different methods to estimate lemming abundance (electronic supplementary material, table S1) but all of these methods were shown to be adequate to monitor lemming population fluctuations [35]. Another line of evidence for that is provided by the abundance of specialized lemming predators, which are known to track local lemming abundance very well. At all sites ($n = 9$) where lemming and predator abundance were

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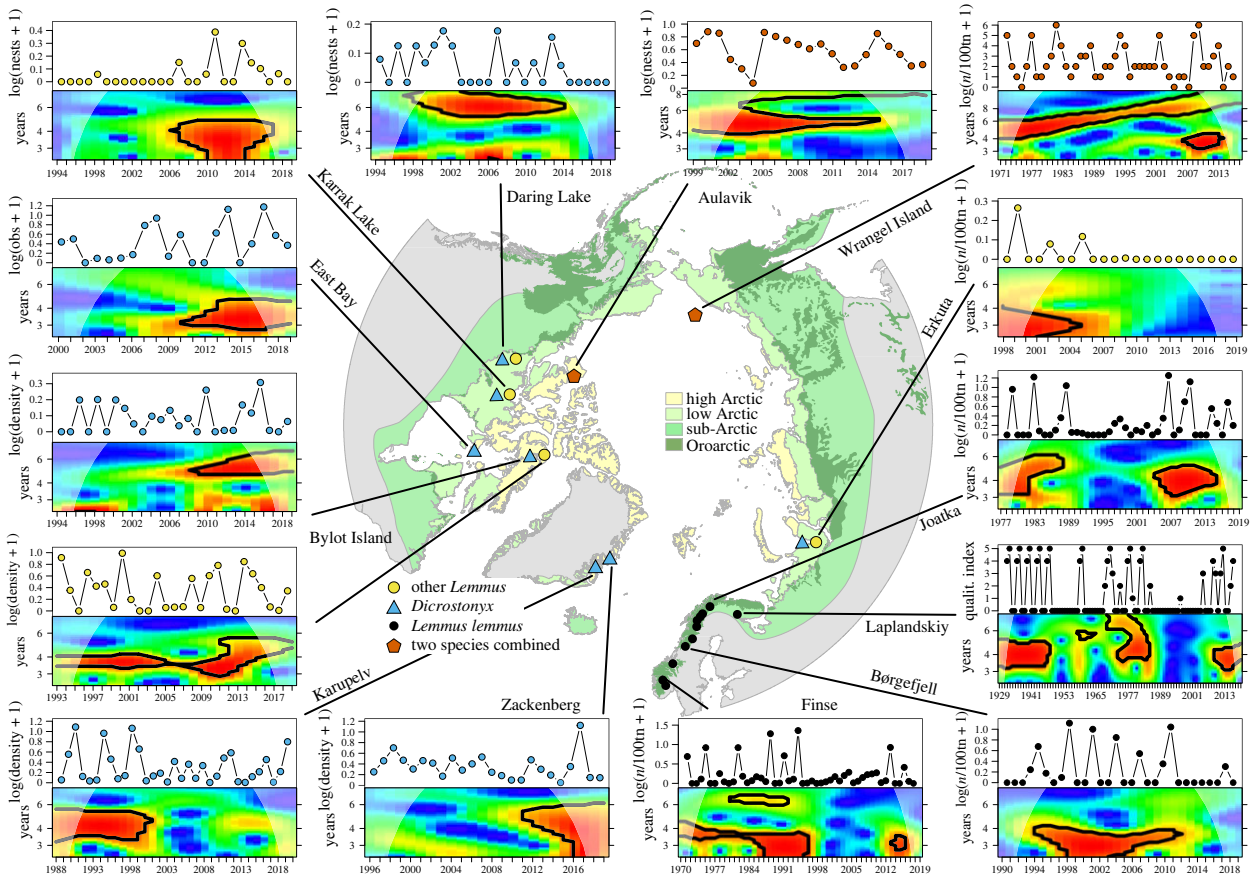


Figure 1. Lemming time series and map of the sites where they were collected. The colours on the map show the bioclimatic subzones of the Arctic [31] and the Oroarctic. For 14 representative time series, the log transformed abundance indices/estimates are shown (colour codes on the time series refer to the species) with results from the wavelet analysis underneath. The colour palette indicates the wavelet power levels from blue to red; red areas with black contour lines show periods with evidence for cyclic dynamics, with the estimated periodicity shown on the *y*-axis. The pale colours at either end of each wavelet plot are outside the cone of influence, an area where results are subject to edge effects. See electronic supplementary material, figure S3 for additional time series.

both monitored, a remarkable concordance between the two was found [4,5,36–41]. See electronic supplementary material, Material and methods and table S2 for details on the methods used to sample lemming abundance and sampling effort.

(b) Wavelet analysis and cyclic pattern

To assess the cyclicity of the lemming time series and possible transient dynamics, we carried out wavelet analyses [42]. Time series were transformed to log(abundance index + 1) [10], except qualitative indices (see electronic supplementary material, Material and methods for justification), and the wavelet power spectrum was calculated using the function *analyze.wavelet* of the package WaveletComp [43] in R v.4.1.3 [44]. The function *analyze.wavelet* applies the Morlet wavelet. We used the option to detrend the time series and the default value of 0.75 for the parameter *loess.span* that determines the degree of smoothing. The significance of periodicity at each time point was assessed from 10 000 simulations and power spectrums were plotted as heat maps showing the contour of significant periods. We used a 0.1 significance level to confirm the presence of cyclic patterns to minimize the risk of inferring the absence of cyclicity in presence of a weak signal. It is also with this significance level that periods of cyclicity that we detected matched most closely those found in previous site-specific analyses at Bylot Island and Finse [18,45,46]. For each time series, we extracted (i) the time over which cyclicity was identified excluding years that were outside the cone of influence and (ii) the periodicity with the highest wavelet power for each year. Mean periodicity was calculated over all time periods in a series for which periodicity was determined to be significant. See electronic supplementary material, Material and methods for more details on calculations.

(c) Climate data

We used temperature data from the ERA5-Land Reanalysis Dataset [47]. This dataset provides hourly temperature data at 2 m above the ground from 1981 to present at a resolution of 0.1° across the globe (approx. 9 km). We extracted temperature data for each of our 20 sites based on their geographical coordinates at 6 h intervals.

We used MODIS snow products [48] (http://nsidc.org/) to assess timing of snow melt and onset of snow at each site for the years 2000–2020 except at Kilpisjärvi where snow data was not available. We aimed to delimit a polygon of *ca* 30 km^2 centred on trapping sites and in relatively homogeneous habitat at each study area to measure snow cover change but in many cases we had to adjust polygon size based on local topography (e.g. to avoid high elevation area or large lakes) or to cover all lemming monitoring plots at sites with multiple plots. Median size of the polygons was 30 km^2 (range: 13–166 km^2; electronic supplementary material, table S2). See electronic supplementary material, Material and methods for details on how the snow data were extracted and for ground validation of snow variables.

We used the snow cover time series and temperature data, either alone or in combination, to define six variables:

Date of snow melt (Melt50): First day in spring when snow cover was equal or less than 50% of the polygon (see electronic supplementary material, figure S1b for an example). We excluded from the calculations apparent early season melting events during which snow cover fell below 50% but returned to cover 100% of the site surface for 5 consecutive days or more. Similarly, we excluded late spring snow precipitation

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events when snow cover returned to 100% for 2 consecutive days or less.

Date of onset of permanent snow cover (Onset80): First day in autumn when snow cover reached or exceeded 80% of the polygon and did not return below 50% at a later date (see electronic supplementary material, figure S2a for an example).

Duration of the snow onset period (Onset_duration): Number of days elapsed between the last day in autumn with a snow cover below 5% of the polygon and the date of onset of permanent snow cover as defined above (Onset80; see electronic supplementary material, figure S2a for an example).

Duration of winter (Winter_length) corresponded to the period with snow and was defined as the number of days elapsed between Onset80 and subsequent Melt50.

Warm spell during snow onset (Warm_onset): Cumulative number of degrees above −2°C (absolute value) per period of 6 h during the period of snow onset as defined above, i.e. Onset_duration (see electronic supplementary material, figure S2b for an example). For instance, a temperature of 2°C for two 6 h period would yield a Warm_onset value of 8.

Warm spell after snow onset (Warm_postonset): Cumulative number of degrees above −2°C (absolute value) per period of 6 h during 30 days after the date of permanent snow onset as defined above (see electronic supplementary material, figure S2b for an example).

Warm spells, as defined above, should promote melt–freeze or rain-on-snow events, conditions known to be detrimental to lemmings (see Introduction). We focused on the period of snow onset and the first 30 days following snow onset because it is when the depth hoar of the basal snow layer, where lemmings live throughout the winter, gets established. Melt–freeze or rain-on-snow events during this period should have the greatest potential to disturb and harden the basal snow layer [34,49]. We chose a threshold of −2°C rather than 0°C because snow temperature below the snow surface during daytime is often greater than air temperature due to the absorption of solar radiation. Based on equations derived by Colbeck [50], we evaluated that snowmelt can take place under sunny conditions when the air temperature is at −2°C or above even at high latitudes in early winter. Since this radiative warming can propagate to depths of at least 10 cm [50], the whole, thin early winter snowpack can be affected by such melt–freeze events. However, our conclusions are not strongly affected by this threshold because repeating the analyses with a threshold value of 0°C rather than −2°C to calculate cumulative number of degrees yielded similar results qualitatively but with smaller effects and wider credible intervals (CIs) (results not shown).

(d) Analyses relating lemming abundance and cyclicity parameters to climate data

First, we investigated the relationships between lemming abundance indices and climate during the previous winter over the period 2000–2020 using a state space model that allowed us to take into account the stochastic sampling variability in each time series. Different observation models were used depending on the observation method used at each site. Snap trapping data, consisting of number of individuals trapped during a certain number of trap nights, were modelled as a Poisson process. Variations in the number of traps used over the years were taken into account as a multiplicative factor. A similar observation model was used for winter nest counts and incidental observations, where variation in the area over which nests were counted or the total number of observation hours were taken into account as a multiplicative factor. For time series resulting from statistical analyses and integrating several sources of data (Bylot Island, Karupelv Valley), sampling variability was modelled with a normal distribution around the mean. Sampling variability of qualitative time series was also modelled as a Poisson process. The process model consisted of a log-linear autoregressive model of order two, a model structure that has been used in numerous studies of cyclic small rodent populations (e.g. [10,51]), and included additional terms representing the possible influence of winter climate on annual population growth as follows:

$$X_{i,t} = a0_i + a1_i \cdot X_{i,t-1} + a2_i \cdot X_{i,t-2} + b \cdot \mathrm{win}_{i,t} + e,$$

where $X_{i,t}$ is the log of lemming abundance in site i at time t, $a0_i$ is a constant specific to the site, $a1_i$ and $a2_i$ are the first and second order autoregressive coefficients (also site specific), b represents coefficients for the effect of variables (win) describing site-specific conditions in the winter preceding summer of year t (win varied between different versions of the model) and e is a normally distributed error term. The coefficients of the autoregressive part of the model (a coefficients) were modelled as site-specific random effects with a global mean. The state space model was implemented in a Bayesian framework (see electronic supplementary material, Material and methods for details and the model script).

We built three variants of the model with different combinations of winter variables corresponding to our two hypotheses: an early winter climate model with variables Warm_onset and Warm_postonset, a winter duration model with variable Winter_length, and an early winter climate + winter duration model (all three variables). These three climatic variables were not strongly correlated (Pearson $r < |0.3|$; electronic supplementary material, table S3). Because of the clear differences in winter climate between the distribution area of *Lemmus lemmus* and that of other lemming species (see electronic supplementary material, Material and methods for details) and some differences in average winter climate among other regions, analyses were carried out using both relative climate data and absolute climate data, both scaled to 0 mean and s.d. of 1 to make effects comparable. Relative values were calculated by subtracting the mean at each site from annual values.

Second, we investigated whether the early winter climate and winter duration differed between periods when the lemming populations were cyclic and when they were not according to the wavelet analysis. We tested for mean differences using linear mixed effect models for each climatic variable (response variable) with cyclicity (cyclic versus non-cyclic) and region (Fennoscandia versus the rest of the Arctic) as fixed effects and times series ID as random effect in the package glmmTMB. For each variable, fixed effects were modelled as additive or as interactive effects. The preferred model was selected with AICc and models that differed by less than 2 in AICc values were considered competitive [52]. Possible temporal autocorrelation of climatic variables was assessed by plotting autocorrelation functions for each site, but no significant pattern was detected (data not shown).

It is also possible that high variability of early winter climate and winter duration, rather than mean suboptimal conditions, leads to periods without lemming cycles. To address this hypothesis, we calculated the standard deviation of each climatic variable for cyclic and non-cyclic periods in each time series. As above, we tested for significant differences in standard deviations for each response variable using linear mixed models.

3. Results

(a) Cyclicity patterns in lemming populations

The 20 sites with time series of lemming population fluctuations covered the circumarctic region with 8 time series located in Canada (5 sites), 2 in Greenland (2 sites), 4 in Russia (3 sites) and 10 in Fennoscandia (10 sites; electronic supplementary material, tables S1 and S2). Individual time

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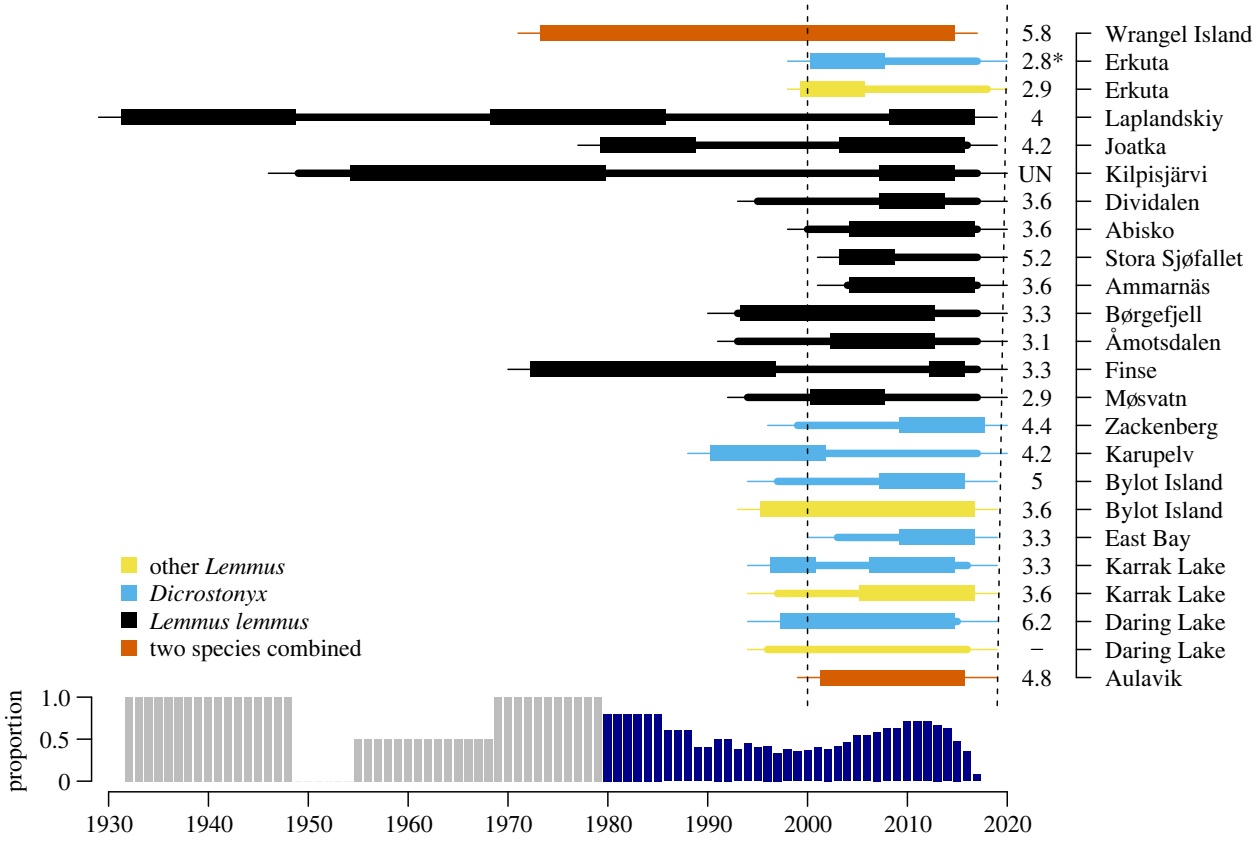


Figure 2. Temporal variation in cyclicity in 24 lemming time series. Thick lines show periods when the time series were characterized as cyclic based on the wavelet analysis whereas thinner lines indicate non-cyclic periods. The very thin lines at both ends of the series represent years outside the cone of influence. The dotted vertical lines indicate the range of years for which climate data were available. The mean periodicity in years is shown for each time series that exhibited cycles. * For *Dicrostonyx* in Erkuta, the periodicity with higher power is reported but there was also a periodicity at 4.3 years; 'UN' for Kilpisjärvi, the periodicity could not be determined. The bar plot at the bottom shows the proportion of time series with cyclic dynamics each year and blue bars represent years with five or more time series. Only time series within the cone of influence were used.

series ranged from 19 to 91 years (median length: 26 years) and included several lemming species: Norwegian lemmings (*L. lemmus*) in Fennoscandia as well as *Dicrostonyx* spp. and other *Lemmus* species at the other sites. Wavelet analysis revealed that all 24 lemming time series except one (*Lemmus* at Daring Lake) showed statistically supported cyclicity in population fluctuations, though in a few cases the cyclic period was short and the pattern rather unclear (e.g. Zackenberg, Stora Sjøfallet; figure 1; electronic supplementary material, figure S3). However, a cyclic pattern was found to be present throughout the study period at only three sites, Wrangel Island, Aulavik (*Lemmus* and *Dicrostonyx* combined at these two sites) and Bylot Island (*Lemmus* only), whereas cyclic patterns disappeared for significant length of time in all other time series (figure 2; electronic supplementary material, table S4).

When considering only years within the cone of influence of the wavelet analyses, 356 study years (all sites pooled) out of 649 (55%) were assigned to cyclic periods (median periodicity: 3.7 years). Disappearance of cycles occurred at different times across sites and there was no evidence that such disappearance was more common in recent years (figure 2; electronic supplementary material, figure S4). Periods with absence of cycles occurred across all lemming taxa (*L. lemmus*, other *Lemmus*, *Dicrostonyx* spp). At five sites (Joatka, Kilpisjärvi, Laplandskiy and Finse for *L. lemmus*; Karrak Lake for *Dicrostonyx*), cycles were discontinuous as they disappeared for some time and reappeared later (figures 1 and 2). There was as much variability in patterns of population fluctuations within as between lemming taxa and geographical regions (Fennoscandia, Russia and North America; figure 1; electronic supplementary material, figure S3).

(b) Climatic influence on lemming population fluctuations

Our analysis of lemming abundance indices in response to climatic variables suggested an influence of early winter climate when using relative climatic variables, in agreement with our early winter climate hypothesis, but not of winter duration (figure 3). The results from the three models were congruent and indicated a negative effect of Warm_onset (−0.183 and −0.174 for the early winter climate model and the early winter climate + winter duration model, respectively) on lemming abundance indices. However, given the high degree of stochasticity inherent to this type of data, posterior CIs were wide and 95% CI included 0 (−0.402, 0.034 for the early winter climate model and −0.397, 0.049 for the early winter climate + winter duration model; figure 3). The mean posterior estimates for Warm_postonset were also negative but indicated a smaller influence (−0.142 and −0.159, respectively) and the 95% CI also overlapped 0 (figure 3). The analyses suggested no influence of winter duration with 50% CI largely overlapping 0. As expected due to clear regional differences in average climate, the effects were less clear when using absolute

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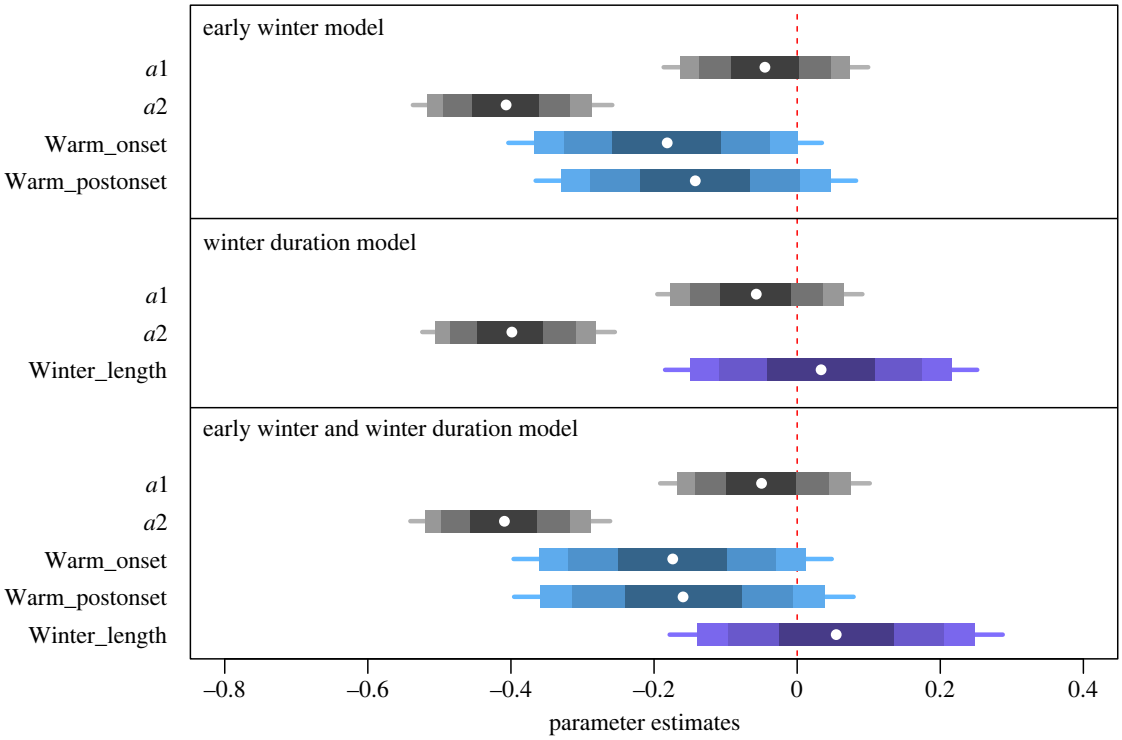


Figure 3. Effect of winter climate on lemming abundance. Parameter estimates for the influence of warm weather in early winter (sum of temperatures above −2°C over periods of six hours) during the period when the snow cover is established (from 5% snow cover to snow cover greater than 80% and not getting reduced to below 50% anymore; Warm_onset) and during the first 30 days after establishment of a permanent snow cover (Warm_postonset), as well as the influence of winter duration (Winter_length) obtained from Bayesian state space models assuming a log-linear autoregressive process of order 2. Climatic variables were scaled to mean 0 and s.d. = 1 prior to analysis making the magnitude of their effects comparable. Autoregressive parameters are shown ($a1$ = direct density dependence +1 (see [10]), $a2$ = delayed density dependence). Results of the three different models correspond to our three hypotheses with climatic variables expressed as relative to the mean at each site. Dots represent the mean of the posterior distribution, boxes the 50%, 80% and 90% credible intervals and lines the 95% credible interval. Red dotted line illustrates 0.

climatic variables, but showed the same overall tendencies (electronic supplementary material, figure S5). All models also revealed congruent direct and delayed density dependence responses. The mean estimate for the autoregressive parameter for direct density dependence (i.e. direct density dependence parameter in a population model +1) was between −0.055 and −0.047 (lower 95% CI: −0.194 to −0.189, higher 95% CI: 0.090 to 0.101) and the estimate for delayed density dependence was between −0.408 and −0.395 (lower and higher 95% CI: −0.543 to −0.522 and −0.262 to −0.247, respectively).

We examined whether early winter climate and winter duration differed on average between cyclic and non-cyclic periods in the lemming time series. However, we found no significant difference in climatic variables between periods with and without lemming cycles as identified by wavelet analysis, both for relative and absolute climatic variables and for the two main biogeographic groups of lemmings (figure 4; electronic supplementary material, figure S6). We also examined annual variability in climatic variable between cyclic and non-cyclic periods. Standard deviations of warm weather following the onset of snow (Warm_postonset) were on average higher ($\beta = 12.3$, 95% CI = 1.9, 22.6) during periods with absence of lemming cycles than during cyclic periods (figure 4; electronic supplementary material, figure S6).

4. Discussion

Our large-scale analysis of lemming dynamics revealed the generality of their cyclic population fluctuations, with a periodicity of 3–4 years most frequently detected despite variation among sites (electronic supplementary material, table S4). More importantly, however, non-cyclic periods were observed in almost all time series, strongly suggesting that cyclicity is a dynamic process in lemmings and that alternating periods of cyclic and non-cyclic fluctuations is common throughout their range. This was also the case for the longest time series ranging from 45 to 91 years originating from subarctic Fennoscandia. Moreover, these non-cyclic periods did not occur synchronously and were not more prevalent in recent years. Therefore, our data do not provide evidence that the fading or collapse of lemming cycles recently reported at some sites [5,18,19] is at present a general phenomenon across the whole Arctic tundra despite repeated suggestions to that effect [53–56]. We recognize, however, the temporal limitation of our dataset, with relatively few series preceding the 1990s.

Angerbjörn *et al.* [16] suggested that episodes of interrupted cyclicity could in fact be low amplitude fluctuations that are not detected by population monitoring (for instance, see Karupelv Valley in recent years; figure 1). This may be especially the case with snap trapping data series or when lemmings are trapped in suboptimal habitats where they may be present only in high density years, as sometimes is the case in Fennoscandia. It is also possible that the large variation in monitoring methods may have reduced the precision of our analysis. However, we note that non-cyclic periods were detected across all the monitoring methods used in this study. Moreover, the key role of lemmings in the tundra food web, either as a driver of predator reproductive success or in impacting tundra vegetation,

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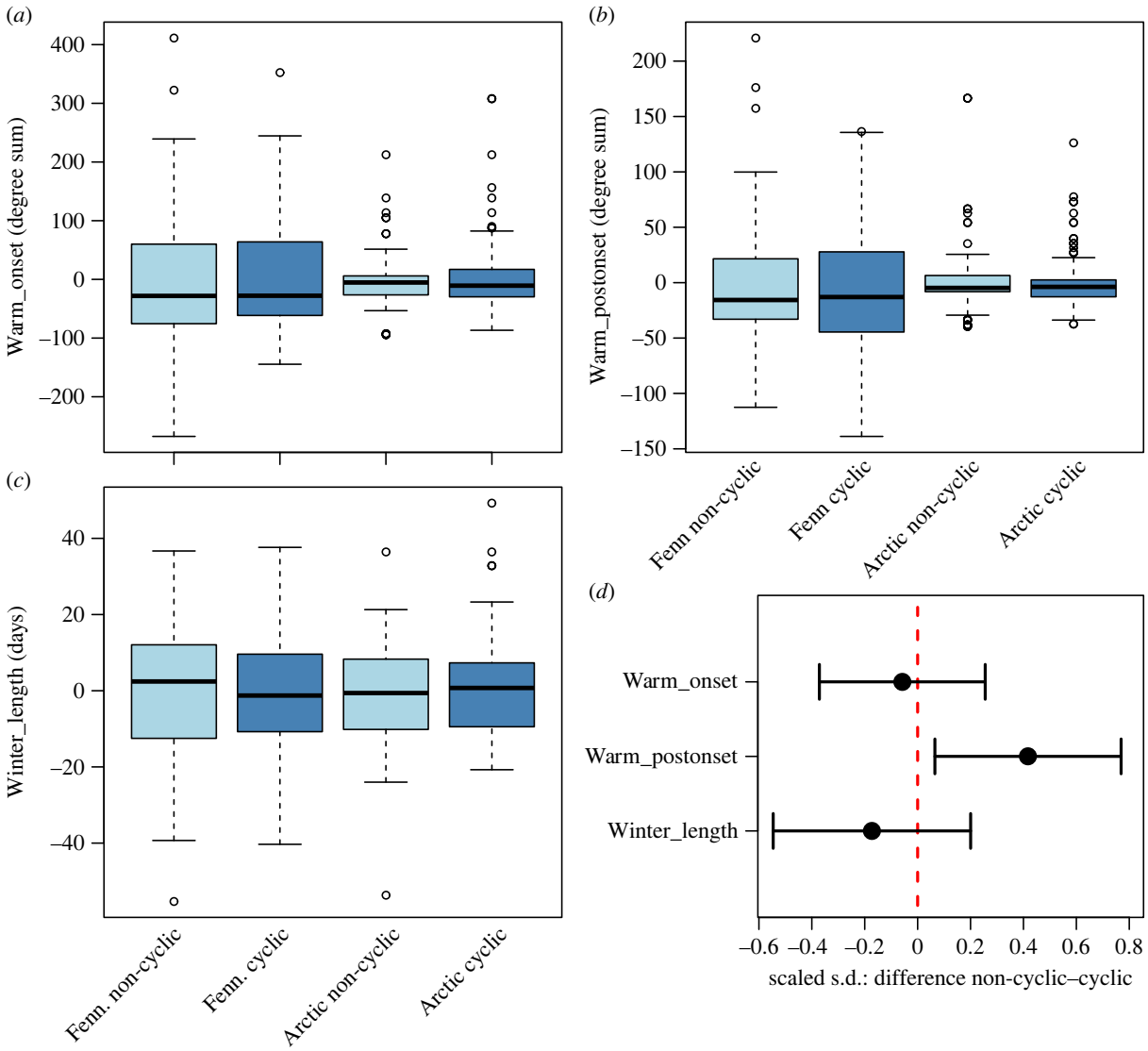


Figure 4. Effect of winter climate on cyclicity of lemming populations. Boxplots of three climatic variables, expressed as relative to the mean at each site, characterizing winter conditions during periods when lemming populations were classified as cyclic or non-cyclic by the wavelet analysis for sites in Fennoscandia (Fenn.) and in the rest of the Arctic (Arctic). The three climatic variables differed between sites with *Lemmus lemmus* in Fennoscandia and sites with other species in the rest of the Arctic (warmer climate and shorter winter in Fennoscandia; electronic supplementary material, figure S7). (*a*) Warm spells during snow onset; (*b*) warm spells during the first 30 days after snow onset and (*c*) winter length. Boxes represent the interquartile distance and horizontal lines show the median. Whiskers show 1.5 times the interquartile range and dots represent values outside this range. (*d*) Differences in standard deviations for each of the three climatic variables (relative values) between non-cyclic and cyclic periods. Standard deviations (s.d.) were scaled to be displayed on the same plot. A positive difference indicates larger climatic variability during non-cyclic periods. Red dotted line illustrates 0.

depends on their populations reaching high absolute densities periodically. Low amplitude fluctuations, such as those observed in several datasets during non-cyclic periods (figure 1; electronic supplementary material, figure S3), cannot fulfil this role [3,36,57].

It remains unclear if the transient dynamics of lemming population fluctuations that we document results from external forcing. Winter climate has been invoked to explain the disappearance of lemming population cycles at some sites. In Greenland, Gilg *et al.* [19] showed that a reduction in the duration of the snow cover due to climate warming could dampen population fluctuations by reducing breeding performance and increasing the period of exposure of lemmings to predators. However, our results do not support this as a general hypothesis as we found no evidence that the duration of the snow cover affects lemming abundance during the following summer at the circumarctic scale. A possible explanation may be that the predator community or the relative importance of predators versus other factors in driving lemming population fluctuations vary across sites [23].

In Fennoscandia, some studies have linked the disappearance of lemming cycles to changing snow conditions in early winter or to warm spells in winter leading to melt–freeze or rain-on-snow events [18,22]. We found support for this hypothesis at the circumarctic scale since the abundance of lemmings was reduced in years following a high occurrence of warm spells with alternating periods of melt and freeze in early winter (i.e. our early winter climate hypothesis). Presence of melting and/or rain-on-snow events during this period should hamper the formation of a soft basal depth hoar in the snowpack, which is detrimental to lemmings [8,34,58]. Presence of such conditions could prevent lemmings from reaching peak densities and potentially lead to highly variable dynamics with irregular peaks. However, the occurrence of warm spells in early winter did not differ on average between periods of cyclic and non-cyclic lemming

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fluctuations in Fennoscandia, where winter climate is the warmest (electronic supplementary material, figure S7), as well as in other regions of the Arctic.

A climate-induced transition from cyclic to non-cyclic dynamics may not be a one-time event but rather may take place over a transient period during which populations alternate between these two regimes in response to climate variability [59]. For periodic population peaks to occur, weather during the pre-peak increase winter appears crucial. A stochastic occurrence of good and bad winters may thus potentially create alternating periods with cyclic and non-cyclic dynamics. Considering that most of our time series started in the 1990s and covered a period when global warming was already impacting the Arctic [28,29,60], the existing time series provide little information to fully investigate this hypothesis. Our observation that increased interannual variability in the occurrence of warm spells following the snow onset was characteristic of periods when cycles disappeared lends support to this hypothesis. However, we note that the transient nature of lemming cycles had been documented based on qualitative data or fur returns of predators for more than a century in Fennoscandia [16,61], before the beginning of global warming. For other parts of the Arctic, previous analyses using the sparse data available suggested varying patterns [55] except for the classic 65-year series of regular cycles based on fox returns in Canada [62].

Environmental stochasticity modulated by the prevailing climatic regime rather than climate warming per se has been suggested to explain the temporary disappearance of vole population cycles in Finland [63,64]. Other environmental changes leading to increased predation or altered food availability have also been suggested for voles in boreal Sweden [65]. Interestingly, Blasius *et al.* [66] reported the occurrence of transient dynamics in a simple planktonic predator–prey system maintained in a stable microcosm as long periods of cyclic oscillations were interspersed by shorter periods characterized by irregular population fluctuations. In this case, the temporary disappearance of cycles was solely due to internal stochastic processes. There is also evidence from modelling work in small mammals that cycles can change or even disappear and reappear solely due to the internal dynamics of the system, even if the environment remains constant [67].

Although our comprehensive analysis of climate impact on lemming population dynamics is the most geographically extensive study so far, we recognize that it is still spatially restricted with respect to the vast circumpolar range of lemmings. In particular, we lacked good quality time series for a large portion of Russia and, to a lesser extent, North America, potentially limiting the generality of our conclusions. Second, even though our analytical method accounted for heterogeneity in observation error, we had to fit the same model structure to all datasets. However, considering that data came from a mix of field methods, species with potentially different ecology, and different ecosystem contexts, it is likely that our model did not fit all time series equally well. For *L. lemmus*, for instance, it has been suggested that a phase-specific density dependent model could be more adequate [10]. Our parameter estimates, aiming at a general picture, thus represent a rather bold averaging of complex ecological processes, but they still provide indications of climatic effects on lemming populations. Finally, we had to use crude proxies of snow conditions based on remote sensing and Reanalysis Datasets at a relatively large spatial scale (approx. 30 km^2) due to the lack of ground measurements at most sites. This limited the precision of our snow data, and potentially our ability to uncover relationships between lemming abundance and snow measurements, but it was the best we could do given data availability. Future studies should aim to collect *in situ* snow measurements (e.g. snow density or hardness, see [68]) or develop snow models capable of predicting specific Arctic snow properties at a relevant spatio-temporal scale [69] to determine more precisely how snow conditions can explain temporal variations in lemming population dynamics as suggested by our analysis.

5. Conclusion

Climate warming is already impacting tundra food webs in several ways [60]. Even though this appears to have led to large-scale dampening of small mammal population fluctuations in boreal regions [1], we found no clear evidence yet that this is affecting the cyclic dynamics of cold-adapted lemmings globally across the circumarctic tundra. Nonetheless, our study adds to the growing evidence that winter climate and especially snow conditions strongly affect population fluctuations of small mammals at high latitudes [8,18,23,64]. Therefore, future climate warming has the potential to destabilize some populations, such as those found in the warmest climate, although the magnitude of these effects could depend on biotic mechanisms driving local population dynamics [23]. However, the transient nature of lemming population cycles documented here makes it difficult to reach definitive conclusions regarding climatic effects on cyclic dynamics. Indeed, ecological systems characterized by cyclic dynamics are prone to prolonged transient behaviour [59] and determining whether non-stationary dynamics is due to internal processes or external forcing such as climate warming is inherently difficult. A comparative approach based on continued long-term monitoring of lemming populations at sites with contrasting climatic regime is essential to resolve these issues in the future but may not be sufficient. Well planed studies examining the links between winter climate and lemming demographic parameters (reproduction, mortality) based on testable predictions and year-round observational data of snow and lemmings are also needed to fully unravel the mechanisms involved. Regardless, despite ongoing climate warming, so far lemming population cycles remain and thereby still play their key ecological functions in the circumarctic tundra.

Ethics. All animal data used in this paper comes from datasets that had already been published elsewhere (see details in electronic supplementary material, tables S1 and S2). No new field data were collected during the preparation of the paper.

Data accessibility. Data used in the study are provided as electronic supplementary material, files (Gauthier_etal_lemmings_cyclicity.txt and Gauthier_etal_lemmings_climate.txt). The content of each file is described in section 'Description of data files' in the electronic supplementary material [70].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.G.: conceptualization, data curation, funding acquisition, project administration, writing—original draft; D.E.: conceptualization, data curation, formal analysis, funding acquisition, writing—original draft; M.B.-B.: formal analysis, writing—original draft; F.D.: conceptualization, writing—review and editing; R.A.: data curation, writing—review and editing; K.C.: data curation, writing—review and editing; F.E.: data curation, writing—review and editing; N.E.E.: data curation, writing—review and editing; E.F.:

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data curation, writing—review and editing; J.F.: data curation; O.G.: data curation, writing—review and editing; H.H.: data curation, writing—review and editing; B.H.: data curation, writing—review and editing; G.D.K.: data curation; I.E.M.: data curation; L.O.: data curation, writing—review and editing; T.O.: data curation, writing—review and editing; J.O.: data curation, writing—review and editing; G.S.: data curation, writing—review and editing; B.S.: data curation, writing—review and editing; P.A.S.: data curation, writing—review and editing; A.A.S.: data curation, writing—review and editing; N.A.S.: data curation, writing—review and editing; N.M.S.: conceptualization, data curation, funding acquisition, writing—original draft.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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