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

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### ► To cite this version:

Gilles Gauthier, Dorothée Ehrich, Maria Belke-Brea, Florent Domine, Ray Alisauskas, et al.. Taking the beat of the Arctic: are lemming population cycles changing due to winter climate?. Proceedings of the Royal Society B: Biological Sciences, 2024, 291 (2016), 10.1098/rspb.2023.2361 . hal-04789243

**HAL Id: hal-04789243**

**<https://hal.science/hal-04789243v1>**

Submitted on 18 Nov 2024

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

3

4 **Running title: Lemming population cycles and winter climate**

5

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54

55 **Abstract**

56 Reports of fading vole and lemming population cycles and persisting low populations in some  
57 parts of the Arctic raised concerns about the spread of these fundamental changes to tundra food  
58 web dynamics. By compiling 24 unique time series of lemming population fluctuations across  
59 the circumpolar region, we show that virtually all populations displayed alternating periods of  
60 cyclic/non-cyclic fluctuations over the past four decades. Cyclic patterns were detected 55% of  
61 the time (N = 649 years pooled across sites) with a median periodicity of 3.7 years and non-  
62 cyclic periods were not more frequent in recent years. Overall, there was an indication for a  
63 negative effect of warm spells occurring during the snow onset period of the preceding year on  
64 lemming abundance. However, winter duration or early winter climatic conditions did not differ  
65 on average between cyclic and non-cyclic periods. Analysis of the time series shows that there is  
66 presently no Arctic-wide collapse of lemming cycles, even though cycles have been sporadic at  
67 most sites during the last decades. Although non-stationary dynamics appears a common feature  
68 of lemming populations also in the past, continued warming in early winter may decrease the  
69 frequency of periodic irruptions with important consequences for tundra ecosystems.

70 **Keywords:** population dynamics, small mammals, transient dynamics, climate warming, Arctic  
71 tundra, melt-freeze events

72

## 73 **1. Introduction**

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

82 Lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) are the most common small rodents of  
83 Arctic tundra and are well known for their large population fluctuations, typically with 3 to  
84 5-year periodicities [10, 11]. Their population fluctuations have become classic textbook  
85 examples of animal population cycles, the causes of which having generated intense debates (see  
86 e.g. [11, 12]), although an emerging consensus points toward delayed density-dependence  
87 governed by trophic interactions [13, 14]. Cyclicity of lemming populations, however, appears  
88 more variable than generally believed as some populations have been found to be non-cyclic or  
89 with irregular fluctuations [5, 15, 16]. In recent decades, major changes in the dynamics of small  
90 mammal populations have been reported in northern Europe [1, 17], and lemming populations  
91 that were previously described as being cyclic have dampened to no or very weak cycles in  
92 Greenland and Fennoscandia [18, 19], a phenomenon coinciding with climate warming. Despite  
93 limited empirical evidence at large spatial scale, fading lemming cycles due to warmer winters,  
94 with dramatic consequences for charismatic predators and the functioning of the food web, have  
95 been used as a prime example of climate change impacts on the Arctic wildlife [20].

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

110 We present the largest circumpolar analysis of lemming populations ever conducted based  
111 on 24 time series from 20 high-latitude sites (figure 1, electronic supplementary material table  
112 S1) where we examine recent changes in their population dynamics. Lemming time series were  
113 carefully selected from [31] to retain only high-quality datasets among those available across the  
114 Arctic region and the Fennoscandian oroarctic mountain areas (see electronic supplementary  
115 material material and methods). We first determined the prevalence of lemming population  
116 cycles across the circumarctic, their dominant periodicity, and the temporal stability of cyclic  
117 fluctuations. We further examined whether climatic conditions during winter could be important  
118 environmental drivers of change in lemming population dynamics across the circumarctic region,

119 as documented at the local scale [18, 19]. We tested two specific hypotheses related to winter  
120 climatic conditions. First, warm temperature during the period of snow onset and shortly after  
121 should promote melt-freeze and rain-on-snow events, which will lead to a hard basal layer in the  
122 snowpack [32, 33]. We hypothesized that a hardened snowpack caused by these early winter  
123 conditions should reduce access to subnivean food and impede lemming reproduction, thereby  
124 limiting population growth over winter and reducing their abundance (*Early winter climate*  
125 hypothesis; [8]). Second, shorter winters should limit population growth and densities the  
126 following summer by reducing the duration of subnivean reproduction and the period that snow  
127 cover protects lemmings from several predators (*Winter duration* hypothesis; [19]).

## 128 **2. Material and methods**

### 129 **(a) Lemming data**

130 The lemming data used in this study were a subset of the population time series assembled from  
131 49 sites across the circumarctic by [31]. We extracted from this dataset the 24 time series (from  
132 20 sites; some sites had data for two different lemming species) that met the following criteria:  
133 (i) they were at least 20 years in length, (ii) data were collected each year during the period 2001  
134 to 2019, (iii) they had a continuous annual record without any gap (in two cases data were  
135 missing for one year: Aulavik 2017 and Åmotsdalen 2018), and (iv) they used a consistent  
136 sampling method with adequate sampling effort throughout the study period. We excluded one  
137 series from southern Sweden (Vålådalen/Ljungdalen) where the lemming index was always very  
138 low except for one year (2011). The criteria applied to select the 24 lemming time series ensured  
139 that we had the datasets of highest quality for our analyses among those compiled by [31] and  
140 available for this key group of species across the circumpolar tundra areas. The time series that  
141 we retained used different methods to estimate lemming abundance (table S1) but all of these



142 methods were shown to be adequate to monitor lemming population fluctuations [34]. Another  
143 line of evidence for that is provided by the abundance of specialized lemming predators, which  
144 are known to track local lemming abundance very well. At all sites ( $n = 9$ ) where lemming and  
145 predator abundance were both monitored, a remarkable concordance between the two was found  
146 [4, 5, 35-40]. See electronic supplementary material, Material and Methods for details on the  
147 methods used to sample lemming abundance and sampling effort (table S2).

#### 148 **(b) Wavelet analysis and cyclic pattern**

149 To assess the cyclicity of the lemming time series and possible transient dynamics, we carried  
150 out wavelet analyses [41]. Time series were transformed to  $\log(\text{abundance index} + 1)$  [10],  
151 except qualitative indices (see electronic supplementary material, Material and Methods for  
152 justification), and the wavelet power spectrum was calculated using the function *analyze.wavelet*  
153 of the package WaveletComp [42] in R vers. 4.1.3 [43]. The function *analyze.wavelet* applies the  
154 Morlet wavelet. We used the option to detrend the time series and the default value of 0.75 for  
155 the parameter *loess.span* that determines the degree of smoothing. The significance of periodicity  
156 at each time point was assessed from 10,000 simulations and power spectrums were plotted as  
157 heat maps showing the contour of significant periods. We used a 0.1 significance level to  
158 confirm the presence of cyclic patterns to minimize the risk of inferring the absence of cyclicity  
159 in presence of a weak signal. It is also with this significance level that periods of cyclicity that  
160 we detected matched most closely those found in previous site-specific analyses at Bylot Island  
161 and Finse [18, 44, 45]. For each time series, we extracted (*i*) the time over which cyclicity was  
162 identified excluding years that were outside the cone of influence, and (*ii*) the periodicity with  
163 the highest wavelet power for each year. Mean periodicity was calculated over all time periods in

164 a series for which periodicity was determined to be significant. See electronic supplementary  
165 material, Material and Methods for more details on calculations.

### 166 (c) Climate data

167 We used temperature data from the ERA5-Land reanalysis dataset [46]. This dataset provides  
168 hourly temperature data at 2m above the ground from 1981 to present at a resolution of 0.1°  
169 across the globe (~9 km). We extracted temperature data for each of our 20 sites based on their  
170 geographic coordinates at 6-h intervals.

171 We used MODIS snow products [47] (<http://nsidc.org/>) to assess timing of snow melt and  
172 onset of snow at each site for the years 2000 to 2020 except at Kilpisjärvi where snow data was  
173 not available. We aimed to delimit a polygon of ca 30 km<sup>2</sup> centered on trapping sites and in  
174 relatively homogenous habitat at each study area to measure snow cover change but in many  
175 cases we had to adjust polygon size based on local topography (e.g. to avoid high elevation area  
176 or large lakes) or to cover all lemming monitoring plots at sites with multiple plots. Median size  
177 of the polygons was 30 km<sup>2</sup> (range: 13 to 166 km<sup>2</sup>; electronic supplementary material table S2).  
178 See electronic supplementary material, Material and Methods for details on how the snow data  
179 was extracted and for ground validation of snow variables.

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

182 Date of snow melt (Melt50): First day in spring when snow cover is equal or less than 50% of  
183 the polygon (see electronic supplementary material figure S1b for an example). We  
184 excluded from the calculations apparent early season melting events during which snow  
185 cover fell below 50% but returned to cover 100% of the site surface for  $\geq 5$  consecutive

186 days. Similarly, we excluded late spring snow precipitation events when snow cover  
187 returned to 100% for  $\leq 2$  consecutive days.

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

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

195 Duration of winter (Winter\_length) corresponded to the period with snow and was defined as  
196 the number of days elapsed between Onset80 and subsequent Melt50.

197 Warm spell during snow onset (Warm\_onset): Cumulative number of degrees  $\geq -2$  °C (absolute  
198 value) per period of 6-hour during the period of snow onset as defined above, i.e.  
199 Onset\_duration (see electronic supplementary material figure S2b for an example). For  
200 instance, a temperature of 2 °C for two 6-h period would yield a Warm\_onset value of 8.

201 Warm spell after snow onset (Warm\_postonset): Absolute value of the cumulative number of  
202 degrees  $\geq -2$  °C per period of 6-hour during 30 days after the date of permanent snow onset  
203 as defined above (see electronic supplementary material figure S2b for an example).

204 Warm spells, as defined above, should promote melt-freeze or rain-on-snow events,  
205 conditions known to be detrimental to lemmings (see introduction). We focused on the period of  
206 snow onset and the first 30 days following snow onset because it is when the depth hoar of the  
207 basal snow layer, where lemmings live throughout the winter, gets established. Melt-freeze or  
208 rain-on-snow events during this period should have the greatest potential to disturb and harden

209 the basal snow layer [33, 48]. We chose a threshold of  $-2\text{ }^{\circ}\text{C}$  rather than  $0\text{ }^{\circ}\text{C}$  because snow  
210 temperature below the snow surface during daytime is often greater than air temperature due to  
211 the absorption of solar radiation. Based on equations derived by [49], we evaluated that  
212 snowmelt can take place under sunny conditions when the air temperature is about  $-2^{\circ}\text{C}$  even at  
213 high latitudes in early winter. Since this radiative warming can propagate to depths of at least 10  
214 cm [49], the whole, thin early winter snowpack can be affected by such melt-freeze events.  
215 However, our conclusions are not strongly affected by this threshold because repeating the  
216 analyses with a threshold value of  $0\text{ }^{\circ}\text{C}$  rather than  $-2\text{ }^{\circ}\text{C}$  to calculate cumulative number of  
217 degrees yielded similar results qualitatively but with smaller effects and wide credible intervals  
218 (results not shown).

#### 219 **(d) Analyses relating lemming abundance and cyclicity parameters to climatic data**

220 First, we investigated the relationships between lemming abundance indices and climate during  
221 the previous winter over the period 2000-2020 using a state space model that allowed us to take  
222 into account the stochastic sampling variability in each time series. Different observation models  
223 were used depending on the observation method used at each site. Snap trapping data, consisting  
224 of number of individuals trapped during a certain number of trap nights, were modelled as a  
225 Poisson process. Variations in the number of traps used over the years were taken into account as  
226 a multiplicative factor. A similar observation model was used for winter nest counts and  
227 incidental observations, where variation in the area over which nests were counted or the total  
228 number of observation hours were taken into account as a multiplicative factor. For time series  
229 resulting from statistical analyses and integrating several sources of data (Bylot Island, Karupelv  
230 valley), sampling variability was modelled with a normal distribution around a mean. Sampling  
231 variability of qualitative time series was also modelled as a Poisson process. The process model

232 consisted of a log-linear autoregressive model of order two, a model structure that has been used  
 233 in numerous studies of cyclic small rodent populations (e.g. [10, 50]), and included additional  
 234 terms representing the possible influence of winter climate on annual population growth as  
 235 follows:

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

236 Where  $X_{i,t}$  is the log of lemming abundance in site  $i$  at time  $t$ ,  $a0_i$  is a constant specific to  
 237 the site,  $a1_i$  and  $a2_i$  are the first and second order autoregressive coefficients (also site specific),  
 238  $b$  represents coefficients for the effect of variables ( $win$ ) describing site specific conditions in the  
 239 winter preceding summer of year  $t$  ( $win$  varied between different versions of the model), and  $e$  is  
 240 a normally distributed error term. The coefficients of the autoregressive part of the model ( $a$   
 241 coefficients) were modelled as site specific random effects with a global mean. The state space  
 242 model was implemented in a Bayesian framework (see electronic supplementary material,  
 243 Material and Methods for details and the model script). We built three variants of the model with  
 244 different combinations of winter variables corresponding to our two hypotheses: an early winter  
 245 climate model with variables Warm\_onset and Warm\_postonset, a winter duration model with  
 246 variable Winter\_length, and an early winter climate + winter duration model (all 3 variables).  
 247 These three climatic variables were not strongly correlated (Pearson  $r < |0.3|$ ; electronic  
 248 supplementary material table S3). Because of the clear differences in winter climate between the  
 249 distribution area of *Lemmus lemmus* and that of other lemming species (see electronic  
 250 supplementary material, Material and Methods for details) and some differences in average  
 251 winter climate among other regions, analyses were carried out using both relative climatic data  
 252 and absolute climatic data, both scaled to 0 mean and standard deviation of 1 to make effects

253 comparable. Relative values were calculated by subtracting the mean at each site from annual  
254 values.

255         Second, we investigated whether the early winter climate and winter duration differed  
256 between periods when the lemming populations were cyclic and when they were not according to  
257 the wavelet analysis. We tested for mean differences using linear mixed effect models for each  
258 climatic variable (response variable) with cyclicity (cyclic versus non-cyclic) and region  
259 (Fennoscandia versus the rest of the Arctic) as fixed effects and times series ID as random effect  
260 in the package glmmTMB. For each variable, fixed effects were modelled as additive or as  
261 interactive effects. The preferred model was selected with AICc and models that differed by less  
262 than 2 in AICc values were considered competitive [51]. Possible temporal autocorrelation of  
263 climatic variables was assessed by plotting autocorrelation functions for each site, but no  
264 significant pattern was detected (data not shown).

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

## 270 **3. Results**

### 271 **(a) Cyclicity patterns in lemming populations**

272 The 20 sites with time series of lemming population fluctuations covered the circumarctic region  
273 with 8 time series located in Canada (5 sites), 2 in Greenland (2 sites), 4 in Russia (3 sites) and  
274 10 in Fennoscandia (10 sites; electronic supplementary material tables S1, S2). Individual time  
275 series ranged from 19 to 91 years (median length: 26 years) and included several lemming

276 species: Norwegian lemmings (*Lemmus lemmus*) in Fennoscandia as well as *Dicrostonyx* spp.  
277 and other *Lemmus* species at the other sites. Wavelet analysis revealed that all 24 lemming time  
278 series except one (*Lemmus* at Daring Lake) showed statistically supported cyclicity in population  
279 fluctuations, though in a few cases the cyclic period was short and the pattern rather unclear (e.g.  
280 Zackenberg, Stora Sjøfallet; figure 1, electronic supplementary material figure S3). However, a  
281 cyclic pattern was found to be present throughout the study period at only 3 sites, Wrangel  
282 Island, Aulavik (*Lemmus* and *Dicrostonyx* combined at these two sites) and Bylot Island  
283 (*Lemmus* only), whereas cyclic patterns disappeared for significant length of time in all other  
284 time series (figure 2, electronic supplementary material table S4).

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

## 296 **(b) Climatic influence on lemming population fluctuations**

297 Our analysis of lemming abundance indices in response to climatic variables suggested an  
298 influence of early winter climate when using relative climatic variables, in agreement with our

309 early winter climate hypothesis, but not of winter duration (figure 3). The results from the three  
300 models were congruent and indicated a negative effect of Warm\_onset (-0.183 and -0.174 for the  
301 early winter climate model and the early winter climate + winter duration model respectively) on  
302 lemming abundance indices. However, given the high degree of stochasticity inherent to this  
303 type of data, posterior credible intervals (CI) were wide and 95% CI included 0 (-0.402, 0.034  
304 for the early winter climate model and -0.397, 0.049 for the early winter climate + winter  
305 duration model; figure 3). The mean posterior estimates for Warm\_postonset were also negative  
306 but indicated a smaller influence (-0.142 and -0.159, respectively) and the 95% CI also  
307 overlapped 0 (figure 3). The analyses suggested no influence of winter duration with 50% CI  
308 largely overlapping 0. As expected due to clear regional differences in average climate, the  
309 effects were less clear when using absolute climatic variables, but showed the same overall  
310 tendencies (electronic supplementary material figure S5). All models also revealed congruent  
311 direct and delayed density dependence responses. The mean estimate for the autoregressive  
312 parameter for direct density dependence (i.e. direct density dependence parameter in a population  
313 model +1) was between -0.055 and -0.047 (lower 95% CI: -0.194 to -0.189, higher 95% CI:  
314 0.090 to 0.101) and the estimate for delayed density dependence was between -0.408 and -0.395  
315 (lower and higher 95% CI: -0.543 to -0.522 and -0.262 to -0.247, respectively).

316 We examined whether early winter climate and winter duration differed on average  
317 between cyclic and non-cyclic periods in the lemming time series. However, we found no  
318 significant difference in climatic variables between periods with and without lemming cycles as  
319 identified by wavelet analysis, both for relative and absolute climatic variables and for the two  
320 main biogeographic groups of lemmings (figure 4, electronic supplementary material figure S6).  
321 We also examined annual variability in climatic variable between cyclic and non-cyclic periods.



322 Standard deviations of warm weather following the onset of snow (Warm\_postonset) were on  
323 average higher ( $\beta = 12.3$ , 95%CI = 1.9, 22.6) during periods with absence of lemming cycles  
324 than during cyclic periods (figure 4, electronic supplementary material figure S6).

#### 325 **4. Discussion**

326 Our large-scale analysis of lemming dynamics revealed the generality of their cyclic population  
327 fluctuations, with a periodicity of 3-4 years most frequently detected despite variation among  
328 sites (electronic supplementary material table S4). More importantly, however, non-cyclic  
329 periods were observed in almost all time series, strongly suggesting that cyclicality is a dynamic  
330 process in lemmings and that alternating periods of cyclic and non-cyclic fluctuations is common  
331 throughout their range. This was also the case for the longest time series ranging from 45 to 91  
332 years originating from sub-Arctic Fennoscandia. Moreover, these non-cyclic periods did not  
333 occur synchronously and were not more prevalent in recent years. Therefore, our data do not  
334 provide evidence that the fading and collapse of lemming cycles recently reported at some sites  
335 [5, 18, 19] is at present a general phenomenon across the whole Arctic tundra despite repeated  
336 suggestions to that effect [52-55]. We recognize, however, the temporal limitation of our dataset,  
337 with relatively few series preceding the 1990s.

338 Angerbjörn et al. [16] suggested that episodes of interrupted cyclicality could in fact be low  
339 amplitude fluctuations that are not detected by population monitoring (for instance, see Karupelv  
340 in recent years, figure 1). This may be especially the case with snap trapping data series or when  
341 lemmings are trapped in suboptimal habitats where they may be present only in high density  
342 years, as sometimes is the case in Fennoscandia. It is also possible that the large variation in  
343 monitoring methods may have reduced the precision of our analysis. However, we note that non-  
344 cyclic periods were detected across all the monitoring methods used in this study. Moreover, the

345 key role of lemmings in the tundra food web, either as a driver of predator reproductive success  
346 or in impacting tundra vegetation, depends on their populations reaching high absolute densities  
347 periodically. Low amplitude fluctuations, such as those observed in several datasets during non-  
348 cyclic periods (figure 1 and electronic supplementary material figure S3), cannot fulfil this role  
349 [3, 35, 56].

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

360         In Fennoscandia, some studies have linked the disappearance of lemming cycles to  
361 changing snow conditions in early winter or to warm spells in winter leading to melt-freeze or  
362 rain-on-snow events [18, 22]. We found support for this hypothesis at the circumarctic scale  
363 since the abundance of lemmings was reduced in years following a high occurrence of warm  
364 spells with alternating periods of melt and freeze in early winter (i.e. our Early winter  
365 hypothesis). Presence of melting and/or rain-on-snow events during this period should hamper  
366 the formation of a soft basal depth hoar in the snowpack, which is detrimental to lemmings [8,  
367 33, 57]. Occasional presence of such conditions could prevent lemmings from reaching peak

368 densities and potentially lead to highly variable dynamics with irregular peaks. However, the  
369 occurrence of warm spells in early winter did not differ on average between periods of cyclic and  
370 non-cyclic lemming fluctuations in both Fennoscandia, where winter climate is the warmest  
371 (electronic supplementary material figure S7), and in other regions of the Arctic.

372 A climate-induced transition from cyclic to non-cyclic dynamics may not be a one-time  
373 event but rather may take place over a transient period during which populations alternate  
374 between these two regimes in response to climate variability [58]. For periodic population peaks  
375 to occur, weather during the pre-peak increase winter appears crucial. A stochastic occurrence of  
376 good and bad winters may thus potentially create alternating periods with cyclic and non-cyclic  
377 dynamics. Considering that most of our time series started in the 1990s and covered a period  
378 when global warming was already impacting the Arctic [28, 29, 59], the existing time series  
379 provide little information to investigate this hypothesis. Our observation that increased  
380 interannual variability in the occurrence of warm spells following the snow onset was  
381 characteristic of periods when cycles disappeared lends support to this hypothesis. However, we  
382 note that the transient nature of lemming cycles had been documented based on qualitative data  
383 or fur returns of predators for more than a century in Fennoscandia [16, 60], before the onset of  
384 global warming. For other parts of the Arctic, previous analyses using the sparse data available  
385 suggested varying patterns [54] except for the classic 65-year series of regular cycles based on  
386 fox returns in Canada [61].

387 Environmental stochasticity modulated by the prevailing climatic regime rather than  
388 climate warming per se has been suggested to explain the temporary disappearance of vole  
389 population cycles in Finland [62, 63]. Other environmental changes leading to increased  
390 predation or altered food availability have also been suggested for voles in boreal Sweden [64].

391 Interestingly, [65] reported the occurrence of transient dynamics in a simple planktonic predator-  
392 prey system maintained in a stable microcosm as long periods of cyclic oscillations were  
393 interspersed by shorter periods characterized by irregular population fluctuations. In this case,  
394 the temporary disappearance of cycles was solely due to internal stochastic processes. There is  
395 also evidence from modelling work in small mammals that cycles can change or even disappear  
396 and reappear solely due to the internal dynamics of the system, even if the environment remains  
397 constant [66].

398         Although our comprehensive analysis of climate impact on lemming population dynamics  
399 is the most geographically extensive study so far, we recognize that it is still spatially restricted  
400 with respect to the vast circumpolar range of lemmings. In particular, we lacked good quality  
401 time series for a large portion of Russia and, to a lesser extent, North America, potentially  
402 limiting the generality of our conclusions. Second, even though our analytical method accounted  
403 for heterogeneity in observation error, we had to fit the same model structure to all datasets.  
404 However, considering that data came from a mix of field methods, species with potentially  
405 different ecology, and different ecosystem contexts, it is likely that our model did not fit all time  
406 series equally well. For *Lemmus lemmus*, for instance, it has been suggested that a phase-specific  
407 density dependence model could be more adequate [10]. Our parameter estimates, aiming at a  
408 general picture, thus represent a rather bold averaging over a certainly more complex variation of  
409 ecological processes, but they still provide indications of climatic effects on lemming  
410 populations. Finally, we had to use crude proxies of snow conditions based on remote sensing  
411 and reanalysis datasets at a relatively large spatial scale (30 km<sup>2</sup>) due to the lack of ground  
412 measurements at most sites. This limited the precision of our snow data, and potentially our  
413 ability to uncover relationships between lemming abundance and snow measurements, but it was

414 the best we could do given data availability. Future studies should aim to collect in situ snow  
415 measurements (e.g., snow density or hardness, see [67]) or develop snow models capable of  
416 predicting specific arctic snow properties at a relevant spatio-temporal scale [68], to determine  
417 more precisely how snow conditions can explain temporal variations in lemming population  
418 dynamics as suggested by our analysis.

## 419 **5. Conclusion**

420 Climate warming is already impacting tundra food webs in several ways [59]. Even though  
421 this appears to have led to large scale dampening of small mammal population fluctuations in  
422 boreal regions [1], we found no clear evidence yet that this is affecting the cyclic dynamics of  
423 cold-adapted lemmings globally across the circumarctic tundra. Nonetheless, our study adds to  
424 the growing evidence that winter climate and especially snow conditions strongly affect  
425 population fluctuations of small mammals at high latitudes [8, 18, 23, 63]. Therefore, future  
426 climate warming has the potential to destabilize some populations, such as those found in the  
427 warmest climate, although the magnitude of these effects could depend on biotic mechanisms  
428 driving local population dynamics [23]. However, the transient nature of lemming population  
429 cycles documented here makes it difficult to reach definitive conclusions regarding climatic  
430 effects on cyclic dynamics. Indeed, ecological systems characterized by cyclic dynamics are  
431 prone to prolonged transient behavior [58] and determining whether non-stationary dynamics is  
432 due to internal processes or external forcing such as climate warming is inherently difficult. A  
433 comparative approach based on continued long-term monitoring of lemming populations at sites  
434 with contrasting climate regime is essential to resolve these issues in the future but may not be  
435 sufficient. Well planned studies examining the links between winter climate and lemming  
436 demographic parameters (reproduction, mortality) based on testable predictions and year-round

437 observational data of snow and lemmings are also needed to fully unravel the mechanisms  
438 involved. Regardless, despite ongoing climate warming, lemming population cycles remain and  
439 thereby still play their key ecological functions in the circumarctic tundra.

440 **Ethics.** All animal data used in this paper comes from datasets that had already been published  
441 elsewhere (see details in tables S1 and S2). No new field data was collected during the  
442 preparation of the paper.

443 **Data accessibility.** Data used in the study are provided as supplementary files  
444 ('Gauthier\_etal\_lemmings\_cyclicality.txt' and 'Gauthier\_etal\_lemmings\_climate.txt'). The content  
445 of each file is provided in section 'Description of data files' in the electronic supplementary  
446 material.

447 **Declaration of AI use.** We did not use AI-assisted technologies in creating this article.

448 **Authors' contributions.** GG, DE, NMS and FD conceptualized the research; everybody except  
449 MBB and FD contributed original data; DE and MBB analyzed data; GG, DE, NMS and MBB  
450 wrote the original draft; everybody reviewed and edited the paper.

451 **Competing interests.** All authors declare no conflict of interest.

452 **Funding.** This work was funded the Natural Sciences and Engineering Research Council of  
 453 Canada (GG), the ArcticNet Network of Centers of Excellence (GG), the Norwegian  
 454 Environment Agency (DE) and the Danish Environmental Protection Agency (NMS). See  
 455 electronic supplementary material table S6 for site-specific funding sources.

456 **Acknowledgements.** We thank the European Center for Medium-Range Weather Forecast  
 457 (ECMWF) and the National Snow and Ice Data Center (NSIDC) for making temperature and  
 458 snow cover data openly accessible and Etienne Godin for his assistance in retrieving the ERA-5  
 459 temperature data.

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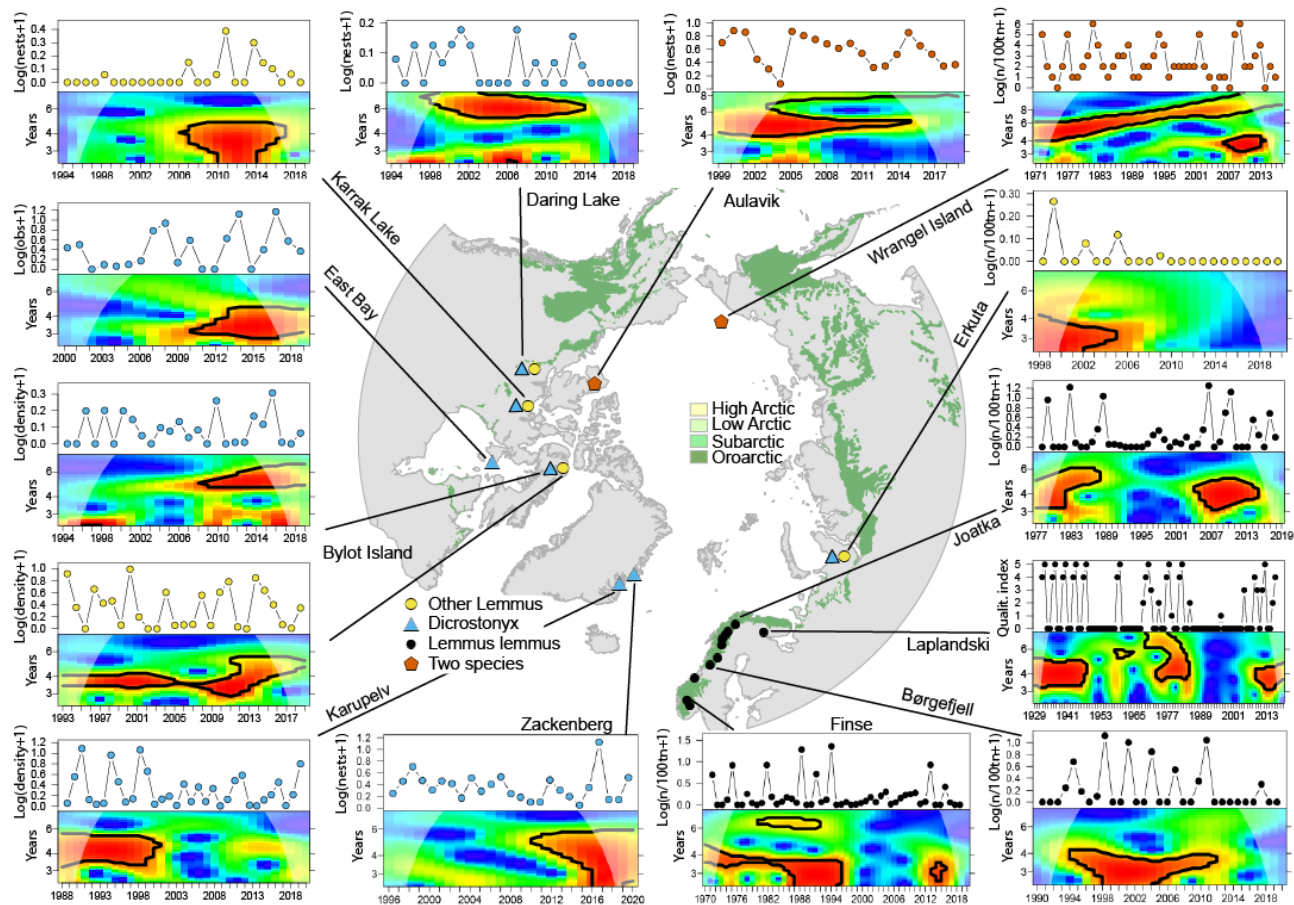
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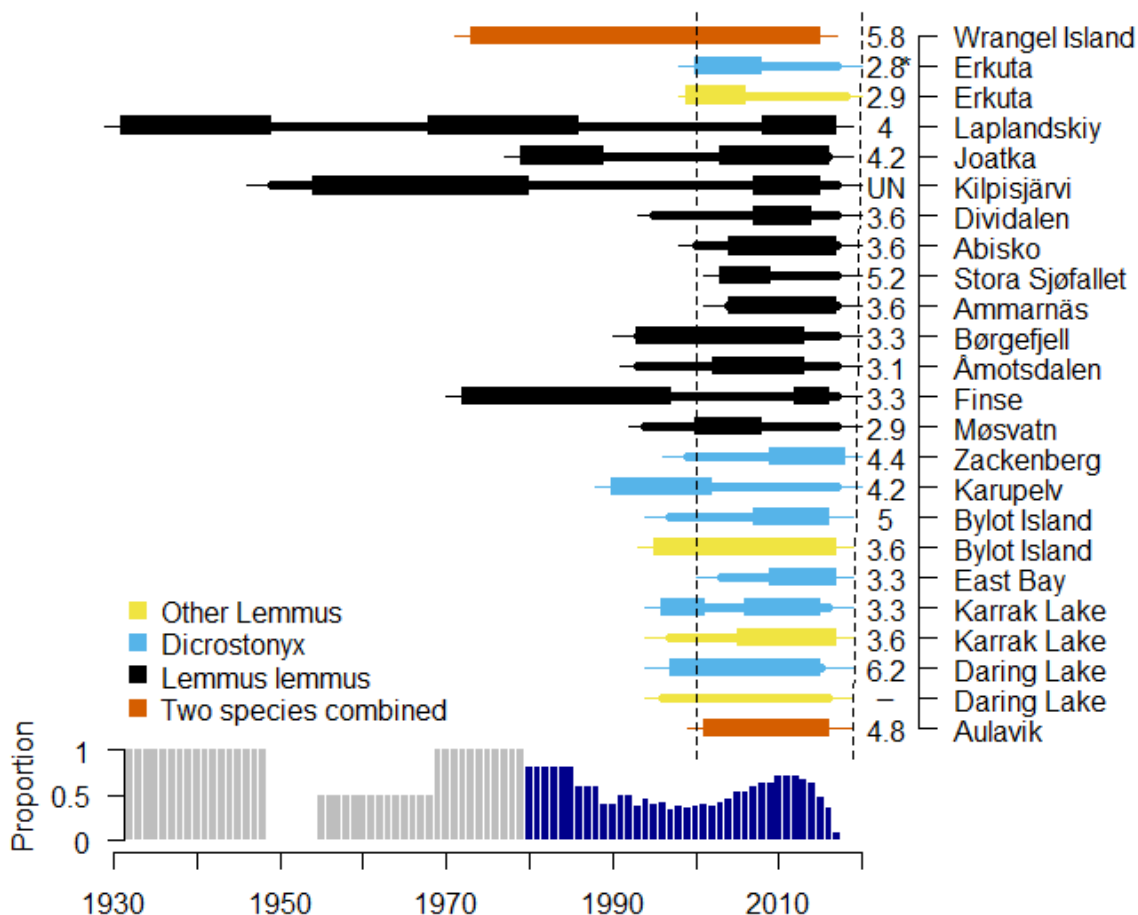
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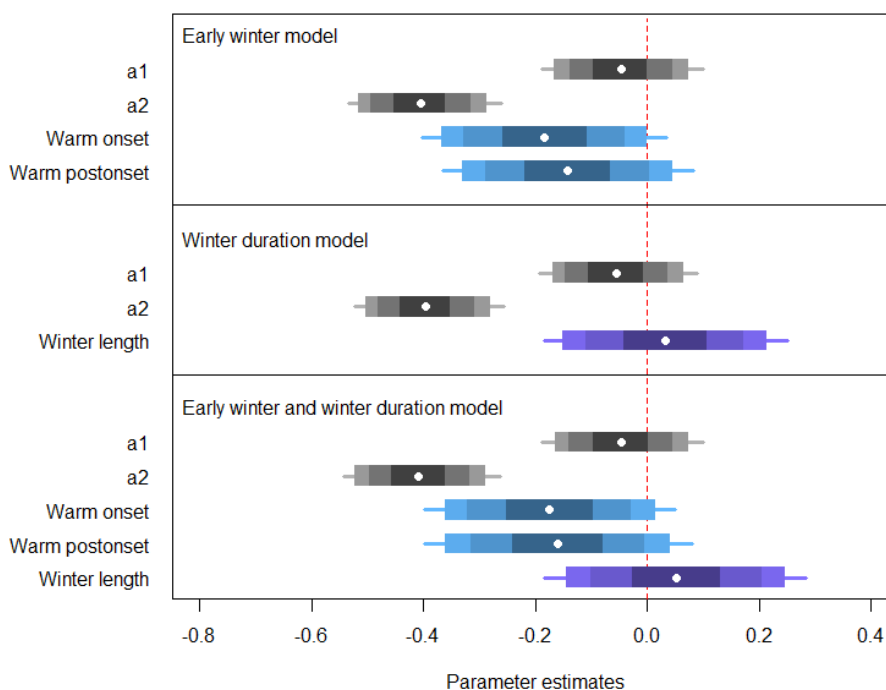
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651 **Figure 1.** Lemming time series and map of the sites where they were collected. The colors on the  
 652 map show the bioclimatic subzones of the Arctic [69] and the Oroarctic. For 14 representative  
 653 time series, the log transformed abundance indices/estimates are shown (color codes on the time  
 654 series refer to the species) with results from the wavelet analysis underneath. The color palette  
 655 indicates the wavelet power levels from blue to red; red areas with black contour lines show  
 656 periods with evidence for cyclic dynamics, with the estimated periodicity shown on the y-axis.  
 657 The pale colors at either end of each wavelet plot are outside the cone of influence, an area  
 658 where results are subject to edge effects. See electronic supplementary material figure S3 for  
 659 additional time series.



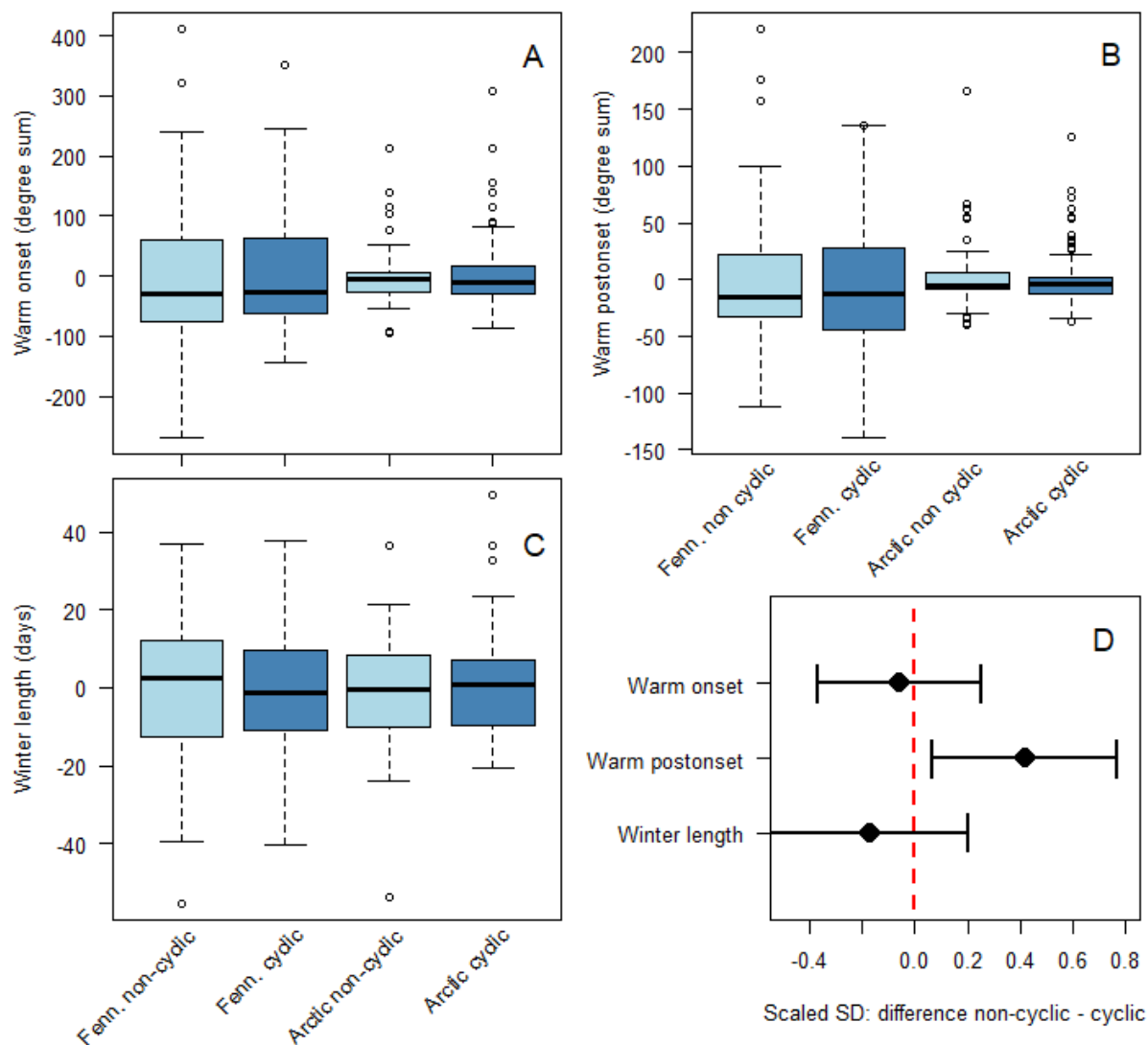
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661 **Figure 2.** Temporal variation in cyclicity in 24 lemming time series. Thick lines show periods  
 662 when the time series were characterized as cyclic based on wavelet analysis whereas thinner  
 663 lines indicate non-cyclic periods. The very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



671  
 672 **Figure 3.** Effect of winter climate on lemming abundance. Parameter estimates for the influence  
 673 of warm weather in early winter (sum of temperatures  $\geq -2$  °C over periods of six hours) during  
 674 the period when the snow cover is established (from 5% snow cover to snow cover > 80% and  
 675 not getting reduced to below 50% anymore; Warm onset) and during the first 30 days after  
 676 establishment of a permanent snow cover (Warm postonset), as well as the influence of winter  
 677 duration (Winter length) obtained from Bayesian state space models assuming a log-linear  
 678 autoregressive process of order 2. Climatic variables were scaled to mean 0 and SD = 1 prior to  
 679 analysis making the magnitude of their effects comparable. Autoregressive parameters are shown  
 680 ( $a1$  = direct density dependence + 1 (see [10]),  $a2$  = delayed density dependence). Results of the  
 681 three different models correspond to our three hypotheses with climatic variables expressed as  
 682 relative to the mean at each site. Dots represent the mean of the posterior distribution, boxes the  
 683 50%, 80% and 90% credible intervals and lines the 95% credible interval.

684



685  
 686 **Figure 4.** Effect of winter climate on cyclicality of lemming population. Boxplots of three climatic  
 687 variables, expressed as relative to the mean at each site, characterizing winter conditions during  
 688 periods when lemming populations were characterized as cyclic or non-cyclic by the wavelet  
 689 analysis for sites in Fennoscandia (Fenn.) and in the rest of the Arctic (Arctic). The three climatic  
 690 variables differed between sites with *Lemmus lemmus* in Fennoscandia and sites with other  
 691 species in the rest of the Arctic (warmer climate and shorter winter in Fennoscandia; electronic  
 692 supplementary material figure S7). A) Warm spells during snow onset; B) Winter duration; C)  
 693 Warm spells during the first 30 days after snow onset. Boxes represent the interquartile distance

694 and horizontal lines show the median. Whiskers show 1.5 times the interquartile range and dots  
695 represent values outside this range. D) Differences in deviations for each of the three climatic  
696 variables (relative values) between cyclic and non-cyclic periods. Standard deviations (SD) were  
697 scaled to be displayed on the same plot. A positive difference indicates larger climatic variability  
698 during non-cyclic periods.  
699