Linking climate change to lemming cycles

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The population cycles of rodents at northern latitudes have puzzled people for centuries[1,2], and their impact is manifest throughout the alpine ecosystem[2,3]. Climate change is known to be able to drive animal population dynamics between stable and cyclic phases[4,5], and has been suggested to cause the recent changes in cyclic dynamics of rodents and their predators[3,6–9]. But although predator–rodent interactions are commonly argued to be the cause of the Fennoscandian rodent cycles[1,10–13], the role of the environment in the modulation of such dynamics is often poorly understood in natural systems[8,9,14]. Hence, quantitative links between climate-driven processes and rodent dynamics have so far been lacking. Here we show that winter weather and snow conditions, together with density dependence in the net population growth rate, account for the observed population dynamics of the rodent community dominated by lemmings (*Lemmus lemmus*) in an alpine Norwegian core habitat between 1970 and 1997, and predict the observed absence of rodent peak years after 1994. These local rodent dynamics are coherent with alpine bird dynamics both locally and over all of southern Norway, consistent with the influence of large-scale fluctuations in winter conditions. The relationship between commonly available meteorological data and snow conditions indicates that changes in temperature and humidity, and thus conditions in the subnivean space, seem to markedly affect the dynamics of alpine rodents and their linked groups. The pattern of less regular rodent peaks, and corresponding changes in the overall dynamics of the alpine ecosystem, thus seems likely to prevail over a growing area under projected climate change.

Winter conditions are likely to be critical for the demography of many high-latitude rodents[7,15,16]. When available, the subnivean space provides thermal insulation, access to food plants and protection from generalist predators like foxes, owls, corvids and raptors[2,16–18]. Norway lemmings and several other Fennoscandian rodents will even commence reproduction in the subnivean if conditions are favourable[2,18]. Changes in the condition and/or duration of the subnivean habitat are thus likely to affect the performance of the rodent community through temperature stress, flooding risk, food limitation and even predator access[2,8,16–20].

Here we combine long-term field estimates of snow conditions with meteorological data to estimate the effect of winter weather fluctuations on snow conditions. Using a 38-year record of rodent trap data (Fig. 1a), we then estimate the effects of snow conditions (Fig. 2a) on the dynamics of the alpine rodent community (Fig. 3), focusing on the numerically dominant lemmings. Using censuses of the local ground-nesting bird communities as well as large-scale data from the annual ptarmigan and willow grouse hunting season, we also assess whether such effects are being transmitted to rodent-linked communities on local and/or regional scales. Wavelet analyses (Fig. 1c–e, Supplementary Figs 10, 11, 14) confirm that all rodents

and birds within our study area had a 3–5-year dominant period in the 1970s and 1980s (that is, before a period of recent warming; see Supplementary Figs 6, 7). The dynamics of both lemmings and other rodents, as well as of the ptarmigan/willow grouse, changed as cyclicity faded in the late 1990s (Fig. 1). With fading cycles, the coherence between lemmings and other rodents abundances also disappeared (1970–1995: $r = 0.70$, $n = 49$, $P < 0.01$; 1996–2007: $r < 0.02$, $n = 22$, $P > 0.50$; see also Supplementary Fig. 14).

Because the formation of subnivean space produces snow crystals with weak cohesion near the ground, the hardness of the bottom of the snowpack is often a good indicator of subnivean conditions[19]. In 15 of the years 1970–2007, this was measured using snow wells dug in late winter (see Methods). The mean measurement is closely negatively correlated with the logarithmic rate of change in total rodent abundance from one spring to the next ($r = -0.80$, $n = 15$, $P > 0.01$; Fig. 2b). The mean number of crusts in the snowpack is closely correlated with the mean measured ground snow hardness ($r = 0.71$, $n = 11$, $P < 0.01$), pointing to the latter being an effect of temperature fluctuations. Indeed, we found that snow hardness for the other 23 years could be predicted from the temperature fluctuations throughout winter (see equations (3) and (4), in Methods), explaining 68% of the observed variance. This predicted hardness was then found to be almost as closely correlated with rodent abundance change over winter ($r = -0.66$, $n = 22$, $P < 0.01$). This is supported by recent experimental evidence that extension of the available subnivean space increases winter survival of the root vole (*Microtus oeconomus*)[16].

Relative air humidity probably reflects significant differences in the amount of free water, and is thus related to heat loss and risk of flooding as well as ice formation[18–20]. This is likely to be important for newborn and lactating females in the subnivean space[8,18]. Indeed, in some winters there appear to have been sizeable populations in late winter that collapsed before spring trapping (E. F., unpublished observations), suggesting a critical spring phase. Rodent abundances—but not rates of change over winter—correlate negatively with relative humidity in April ($r = -0.52$, $n = 24$, $P < 0.01$) measured at Finse meteorological station. It has been suggested[2] that successful spring reproductive phases for the rodent species that start reproducing under the snow contribute to high summer peaks by swamping generalist predators. We modelled fourteen years (1991, 1995–2007) of humidity data using temperature and precipitation (see equation (5), in Methods), and found that they explained 74% of the observed variance. Most of the negative correlation between April humidity and rodent density stems from the fact that five of the six rodent peak years for which humidity measurements are available had median relative humidities of less than 81%, and values this low are predicted not to have occurred since 1996 (Fig. 2). Indeed, a significantly higher median April humidity is predicted after this time (difference between the

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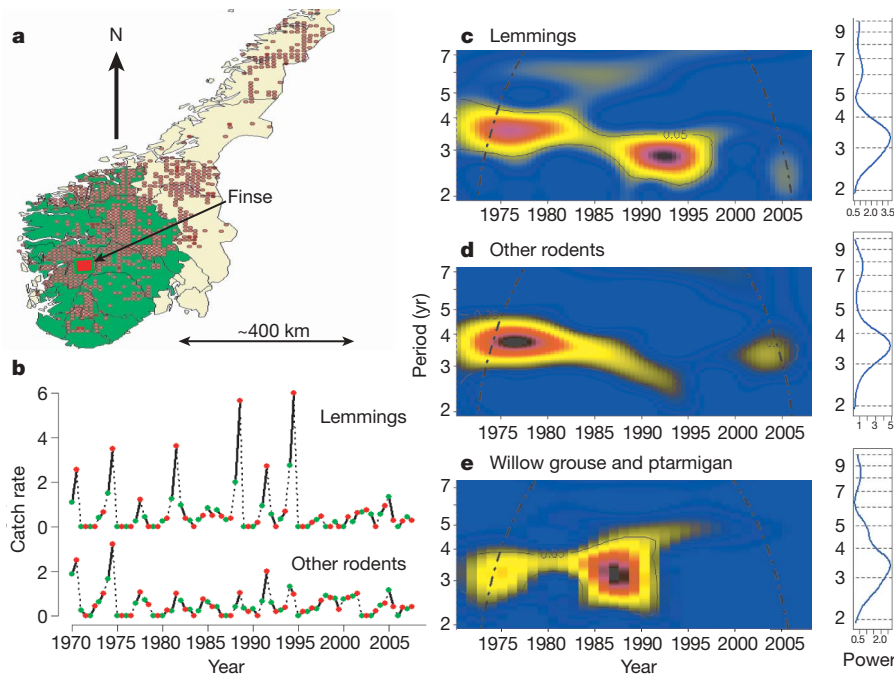
Figure 1 | Population time series. a, Map of South Norway, showing lemming distribution (brown; see http://www.zoologi.no/patlas/kart/lemen.gif), Finse (red) and counties overlapping the central massif (green). **b**, The rodent catch rates at Finse (green, spring; red, fall; for clarity, we display the square roots of the data). All catch rates are expressed as number caught per 100 trap nights. **c–e**, Wavelet power spectra showing the periodicity of the Finse lemmings (**c**) and other rodents (**d**), and logarithmic rate of change in the ptarmigan and willow grouse hunting returns over the counties highlighted in **a** (**e**). Shifts in periodicity are evident inside the 95% confidence areas (solid black line) and cone of influence (broken black line) (see Methods). Time-averaged spectra show the dominance of the three- to four-year period.

1970–1997 mean and the 1998–2007 mean, 5 percentage points; 18 degrees of freedom, $P > 0.001$). Accordingly, the correlation between humidity and rodent abundance disappears after the last rodent peak of 1994.

To look for effects of the duration and magnitude of snow cover *per se*, we used field estimates of the percentage of ground still covered by snow in mid-July. We found that the North Atlantic Oscillation (NAO; see Methods and Supplementary Information),
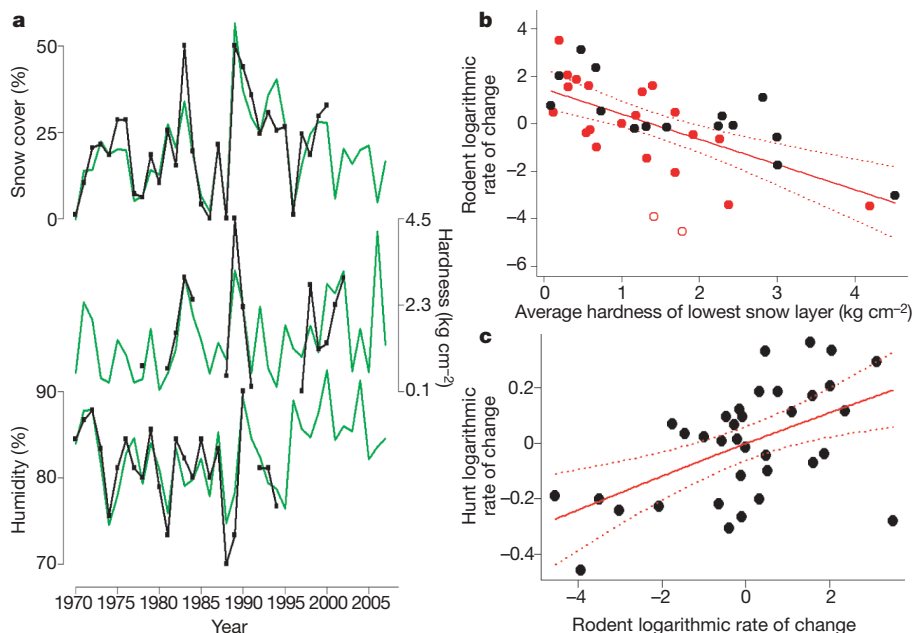

Figure 2 | Climate. a, Data (black) and modelled proxies (green) for the environmental variables found to affect rodent dynamics. **b**, Logarithmic rate of change in rodent abundance, plotted against ground snow hardness. The relationship holds both for observations (black) and the independently modelled proxies based on winter climate (red). The data for 1974–1975 and 1994–1995 (open circles) have the highest rodent populations in the first spring, so these two points slightly lower (but parallel) to the others are expected from predator responses. **c**, Logarithmic rate of change in rodent catch rates at Finse, plotted against the logarithmic rate of change in South Norway ptarmigan and willow grouse hunting returns (Fig. 1 and Supplementary Information).

together with the mean temperatures for October, May and June, explains about 87% of the observed variance (see equation (6), in Methods). Also, the predicted duration of snow cover was not found to be correlated with rodent population growth, but was still found to be a moderately significant explanatory variable in rodent population models (equations 1 and 2).

As global temperatures are expected to rise, we note that temperature is a highly significant predictor of hardness, humidity and duration of the snow cover.

Although spring and autumn densities of rodents are closely correlated ($r = 0.74$, $n = 38$, $P < 0.01$), spring density is linearly independent of the preceding autumn ($r = 0.09$, $n = 38$, $P > 0.50$). Thus, events between autumn and spring seem to be key to predicting between-year fluctuations. By incorporating winter conditions into statistical population models (see equations (1) and (2) and Fig. 3; Methods and Supplementary Information) for the rodent abundance dynamics between 1970 and 1997, we observe that humidity and hardness seem to have strong effects on the over-winter abundance trajectory: together with the previous year's rodent abundances, they are capable of explaining the spring catch rates. The duration of snow cover has considerably less effect (Fig. 3). The autumn abundances, on the other hand, are usually well explained by the spring abundances, with less direct impact from winter conditions.

Despite having predominantly stable mean-field equilibrium, the dynamic behaviour of the models (equations (1) and (2) under environmental stochasticity are consistent with 'cycles' of three to five or more years). This may reconcile the traditional view of rodent fluctuations as limit cycles with the seemingly chaotic dynamics exhibited by several lemming populations[21,22]. The stochastic dynamics captured by our models (see Fig. 3 and Methods) show that the frequency distributions of winter weather variables profoundly influence dynamics without invoking values beyond the observed range. Skewing the distributions of hardness and/or humidity towards increasing values changed the dynamics from three- to five-year cycles towards less frequent peaks and predominantly low-amplitude fluctuations (Fig. 3). The effect of snow duration on cyclicity seemed markedly lower, consistent with the Fennoscandian rodents exhibiting cyclical

tendencies and responses to changing snow conditions over a wide range of altitudes and, thus, snow cover durations.

Notably, the predicted dynamical behaviour emerges from models trained only on 1970–1997 population data. Thus, our predictions do not derive simply from contrasting climate before and after the dynamical shift in the late 1990s, but predicts the absence of rodent peaks after 1994 from the behaviour of the system up to that point.

The logarithmic rate of density change in the local passerine and wader communities (see Methods) are highly correlated with the logarithmic rate of change in rodent density from one spring to the next ($r = 0.69$, $n = 15$, $P < 0.01$ for rodents versus passerines; $r = 0.64$, $n = 14$, $P = 0.01$ for rodents versus waders). Although the ptarmigan and willow grouse data (see Fig. 1 and Methods) was gathered on a much larger spatial scale than the rodent data, there is a high correlation between the logarithmic rate of change in annual rodent abundance at Finse and the logarithmic rate of change in hunting success in the counties overlapping the Hardangervidda massif ($r = 0.65$, $n = 35$, $P < 0.01$; Fig. 1). This correlation stays constant over time, and is reflected in the transition from a three-year period to aperiodicity in the ptarmigan and willow grouse time series in the early 1990s (Fig. 1e). Detrending the ptarmigan and willow grouse data (see Methods and Supplementary Information), we moreover find support for the old observation that there is a positive correlation between the ptarmigan/willow grouse and rodent densities ($r = 0.64$, $n = 36$, $P < 0.01$), even on these different scales. Analysing the counties separately reveals the same pattern (Supplementary Table 5 and Supplementary Fig. 14).

The strong correlations between the annual growth rates of the rodent and different bird communities are consistent with shared predators being an important part of the cyclic and synchronous behaviour of the system[11,18,23], although snow hardness may also have a direct effect on ptarmigan and willow grouse (see Supplementary Fig. 9). Modelling lemmings and other species separately supports the idea that the negative density-dependence term should include all rodent species, despite their different food niches, probably because the reproductive success of many predators depends closely on total rodent abundance[2,6] (even though other agents, like diseases[24,25], may
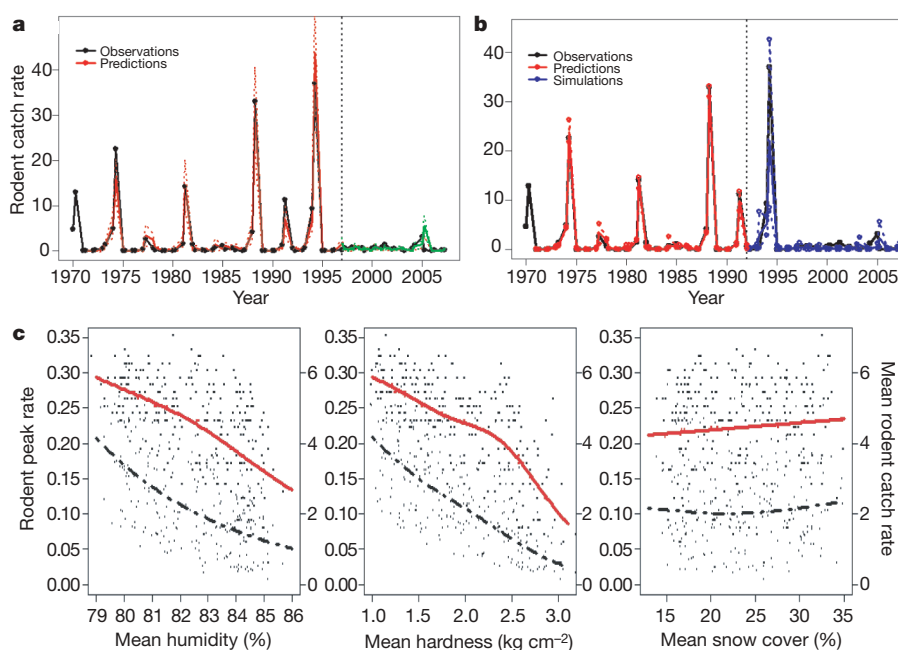

Figure 3 | Models. a, Rodent catch rates with population models (equations (1) and (2)) trained on 1970–1997 data. Black, observations; red, fitted values; green, predictions for 1998–2007. Broken lines indicate the 95% confidence interval of the fit. **b**, As in **a**, but with models trained on 1970–1992 data and the population trajectory simulated for 1992–2008, using (proxy) climate data (blue). The 1994 peak and subsequent absence of peaks are captured. In **b**, the dotted blue line indicates the 95th percentile from 10^3 stochastic simulations. **c**, The climate effects captured by the model: mean rodent peak-year frequencies (red) and mean catch rates (black, small dots) from 10^3 simulations skewing one of the frequency distribution of an environmental variable.

also be involved). The effect seems consistent with the numerical response curve of stoats (*Mustela erminea*) estimated in ref. 26. Specialist predators like stoat and the least weasel (*Mustela nivalis*) can be efficient predators under the snow[16,27] and have highly adapted reproduction strategies tying the number of offspring closely to prey abundance, giving a strongly nonlinear numerical response[26,27]. Although the issue is still debated[28], their numerical response is probably a key causal link between rodent demography and system dynamics.

The abundance relationship between lemmings and the other rodent species suggests that lemming numerical dominance is a result of the extreme peaks, when the lemmings seem to out-reproduce all other species under ideal winter conditions (the correlation between lemming proportion and total catch rate is $r = 0.41$, with $n = 38$, $P < 0.05$). This is responsible for the negative correlation between snow hardness and the proportion of lemmings in the total catch rate ($r = -0.41$, $n = 38$, $P < 0.05$). Lemmings are well known to have very low low-phase population densities, so it is reasonable to expect[4] a decreasing proportion of lemmings in the rodent community when winter conditions remain adverse over time.

The large-scale coherence (see Supplementary Fig. 14) between ptarmigan/willow grouse and rodents is consistent with the considerable spatial autocorrelation in the climate effects, which should have a partial, probabilistic, phase-locking effect on rodent populations over a large area, with corresponding effects on predator-linked species like ptarmigan and willow grouse. However, we expect this to decouple as deteriorating winter conditions decreases the probability of rodent (sub)populations peaking, resulting in less frequent, more local rodent years and correspondingly less potent 'predator pulses' to structure the alpine food web dynamics in space and time. These findings seem consistent with observed spatial and temporal gradients in rodent dynamics, and with the hypothesis[8,21] that snow cover influences the interaction between rodents and specialist (mustelid) versus generalist predators, but indicate that the dynamical effects of predation are dependent on climate-linked processes (see Fig. 4).

Climate reconstructions suggest that the increasingly warm late winter/early spring periods in southeastern Norway over the last decades are unprecedented since 1756[29], when records began. Ongoing climate change may bring more precipitation and higher temperatures[30], and thus probably increase humidity and hard snow over the Scandinavian peninsula, which again will cause the lemming cycle to cease. We can currently only speculate that the absence of occasional or periodic extreme rodent grazing will affect the competitive balance of functional plant groups, with subsequent changes in

nutrient cycling. But considering the likely importance of resource pulses for persistence in a poor environment[4], it is probable that the absence of regularly occurring large-scale rodent peak years is responsible for the dramatic declines in arctic foxes and snowy owls on the Scandinavia peninsula[3,9]. On a general level, this points to the fact that environmental changes may perturb any system away from the range of conditions over which it is cyclic. Also, in so far as many naturally occurring cycles involve specialist interactions, which may take time to adjust by migration, demography and/or evolution as communities change, new cycles may appear at a slower rate when the environment changes as quickly as currently seems to be the case.

METHODS SUMMARY

The observed catch rate, $z_{x,t}$ (rodents caught per 100 trap nights), for season x in year t is assumed to be an unbiased measure proportional to the unobserved rodent abundance, where $n_{x,t} = \ln(z_{x,t} + \tau_{1,t})$ and the transformation parameter τ is Beta(β_1, β_2) distributed (see Supplementary Information). The parameter τ represents low, random, abundances when no animals were caught. All statistics reported here are the mean results over at least 10^3 random series of τ. By H_t, U_t, and K_t we respectively denote the ground snow hardness, the relative humidity in April and the percentage snow cover in July.

We then fit a statistical population model describing the seasonal rodent abundance fluctuations:

$$z_{s,t} = \exp\left(\alpha_0 + \alpha_1 n_{a,t-1} + \alpha_2 h_t + \alpha_3 u_t + f_1(n_{s,t-1}) + \varepsilon_{s,t}\right) \quad (1)$$

$$z_{a,t} = \exp\left(\alpha_4 + \alpha_5 n_{a,t-1} + \alpha_6 k_t + \alpha_7 u_t + f_2(n_{s,t}) + \varepsilon_{a,t}\right) \quad (2)$$

Here $h_t = \ln(H_t + c_1)$, $k_t = \ln(K_t + c_2)$, $u_t = \ln(U_t)$, c_1 and c_2 are transformation constants, $f_x(y)$ represent nonlinear effects estimated from penalized regression splines (see Methods and Supplementary Information), $\varepsilon_{x,t}$ are quasi-Poissonian noise terms to allow for overdispersion, and $\alpha_0, \ldots, \alpha_7$ are estimated regression coefficients.

We find this to be an adequate model for the Finse rodents: it explains about 90% of the observed variance in catch rates when trained on the 1970–1997 data, correctly identifies all peak years with no false positives between 1970 and 1997 when doing one-step-ahead predictions, and correctly predicts an absence of peaks between 1998 and 2007, owing to its correctly predicting low spring abundances ($r = 0.70$, $n = 10$, $P < 0.05$). No significant serial autocorrelations were observed in the residuals of the seasonal models. Even when trained only on 1970–1990 data, this population model captures the peak years 1991 and 1994, as well as the absence of peaks thereafter.

Autumn catches are not well predicted in the low-abundance period, 1995–2008, as they are much more weakly coupled to spring catches during this period (spring–autumn 1970–1995: $r = 0.81$, $n = 26$, $P < 0.01$; 1996–2007: $r = 0.28$, $n = 12$, $P > 0.2$), but see Supplementary Information.

Model validation was performed by fitting on parts of the data set and predicting the remaining part, both by one-step-ahead predictions and multi-year simulations. The models exhibit mostly stationary dynamical behaviour over time. Model coefficients and diagnostics are given in the Supplementary Information.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.
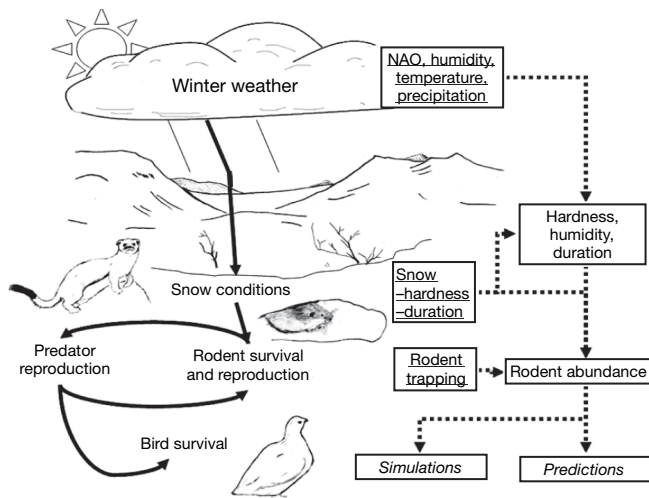
Figure 4 | Overview. Underlined text indicates available data, used in models (boxes) linking meteorological data, snow conditions and population dynamics. The resulting inferences (dotted lines) are consistent with processes (solid arrows) likely to be important for ecosystem dynamics.

1. Stenseth, N. C. The long-term study of voles, mice and lemmings: homage to Robert Collett. *Trends Ecol. Evol.* **10**, 512 (1995).
2. Stenseth, N. C. & Ims, R. A. (eds) *The Biology of Lemmings*. (Academic, 1993).
3. Ims, R. A. & Fuglei, E. Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* **55**, 311–322 (2005).
4. Holt, R. D. Theoretical perspectives on resource pulses. *Ecology* **89**, 671–681 (2008).
5. Coulson, T. *et al.* Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1499–1500 (2001).
6. Framstad, E., Stenseth, N. C., Bjørnstad, O. N. & Falck, W. Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence. *Proc. R. Soc. Lond. B* **264**, 31–38 (1997).
7. Hörnfeldt, B. Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. *Oikos* **107**, 376–392 (2004).
8. Hörnfeldt, B., Hipkiss, T. & Eklund, U. Fading out of vole and predator cycles? *Proc. R. Soc. B* **272**, 2045–2049 (2005).
9. Ims, R. A., Henden, J. A. & Killengreen, S. T. Collapsing population cycles. *Trends Ecol. Evol.* **23**, 79–86 (2008).

10. Klemola, T., Pettersen, T. & Stenseth, N. C. Trophic interactions in population cycles of voles and lemmings: a modelling study and a review-synthesis. *Adv. Ecol. Res.* **33,** 75–160 (2003).

11. Steen, H. *et al.* Mortality of lemmings, *Lemmus lemmus*, at peak density in a mountainous area of Norway. *J. Zool.* **243,** 831–835 (1997).

12. Turchin, P. & Hanski, I. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol. Lett.* **4,** 267–276 (2001).

13. Strann, K.-B., Yoccoz, N. G. & Ims, R. A. Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. *Ecography* **25,** 81–87 (2002).

14. Bierman, S. N. *et al.* Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (*Microtus agrestis* L.). *Am. Nat.* **167,** 583–590 (2006).

15. Aars, J. & Ims, R. A. Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. *Ecology* **83,** 3449–3456 (2002).

16. Korslund, L. & Steen, H. Small rodent winter survival: snow conditions limit access to food resources. *J. Anim. Ecol.* **75,** 156–166 (2006).

17. Lindström, E. R. & Hörnfeldt, B. Vole cycles, snow depth, and fox predation. *Oikos* **70,** 156–160 (1994).

18. MacLean, S. F., Fitzgerald, B. M. & Pitelka, F. A. Population cycles in Arctic lemmings: winter reproduction and predation by weasels. *Arctic and Alpine Research* **6,** 1–12 (1974).

19. Marchand, P. J. *Life in the Cold: An Introduction to Winter Ecology* (University Press of New England, 1996).

20. Merritt, J. F. & Merritt, J. M. Population ecology and energy relationships of Clethrionomys gapperi in a Colorado subalpine forest. *J. Mamm.* **59,** 576–598 (1978).

21. Oksanen, L. & Oksanen, T. Long-term microtine dynamics in North Fennoscandian tundra – the vole cycle and the lemming chaos. *Ecography* **15,** 226–236 (1992).

22. Stenseth, N. C., Chan, K.-S., Framstad, E. & Tong, H. Phase- and density-dependent population dynamics in Norwegian lemmings: Interaction between deterministic and stochastic processes. *Proc. R. Soc. Lond.* **265,** 1957–1968 (1998).

23. Hanski, I. *et al.* Small-rodent dynamics and predation. *Ecology* **82,** 1505–1520 (2001).

24. Niklasson, B. *et al.* Diabetes and myocarditis in voles and lemmings at cyclic peak densities – induced by Ljungan virus? *Oecologia* **150,** 1–7 (2006).

25. Anderson, R. M. & May, R. M. Population biology of infectious diseases: Part I. *Nature* **280,** 361–367 (1979).

26. Gilg, O. *et al.* Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos* **113,** 193–216 (2006).

27. Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos* **50,** 353–365 (1987).

28. Lambin, X., Bretagnolle, V. & Yoccoz, N. G. Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern? *J. Anim. Ecol.* **75,** 340–349 (2006).

29. Nordli, Ø., Lundstad, E. & Ogilvie, A. E. J. A late-winter to early-spring temperature reconstruction for southeastern Norway 1758 to 2006. *Ann. Glaciol.* **46,** 404–408 (2007).

30. Hanssen-Bauer, I., Førland, E. J., Haugen, J. E. & Tveito, O. E. Temperature and precipitation scenarios for Norway: comparison of results from dynamical and empirical downscaling. *Clim. Res.* **25,** 15–27 (2003).

METHODS

Statistical analyses. The strong seasonality of the system suggests that discrete time dynamics are applicable[31], and we assume that ease of trapping is unbiased through time, as trapping has taken place in the same survey programme in permanent plots of stable vegetation (see Supplementary Information). There is no significant between-year autocorrelation in the lemming spring densities, and only at year $t-2$ for the autumn densities ($r = -0.47$, $n = 38$, $P < 0.01$), where n denotes the number of data pairs.

We used generalized additive models (GAMs) with integrated smoothness estimation using penalized regression splines. In all GAMs, the nonlinear functions were constrained to have monotonic behaviour. Quasi-Poissonian error distributions were used to allow for overdispersion. To avoid noise and potential bias from the proxy humidity data, the GAMs were fitted on only the 1970–1997 data. None of the partly continuous environmental time series (temperature anomalies, snow cover, NAO and humidity) exhibited any significant between-year autocorrelation over the period 1969–2007, and the population model residuals were free from temporal autocorrelation.

The significance of the hardness and humidity covariates and their dynamical effects are robust over a variety of model formulations and approaches, including Bayesian state-space modelling. Temperature and NAO measures were also tried directly as covariates, but on the whole were found to perform worse and less robustly than the snow parameters, as would be expected if these were closer to the actual mechanisms.

All effects are, unless otherwise noted in the text, significant at the 5% level or less. Parameter tables and model diagnostics can be found in the Supplementary Information. Wavelet analyses using a Morlet wavelet and Beta surrogate significance test[32] were performed to assess changes in periodicity and coherence[33]. Analyses were performed using the software R (http://www.r-project.org).

Time series data on rodents and birds. The rodent data are 38-yr-long, seasonal trapping series from Finse, which is situated in the Hardangervidda massif of southern Norway (Fig. 1a) between 1200–1350 metres above sea level in the low- and mid-alpine zones[34]. Small mammals were monitored through trapping in two 1×1-ha^2 grids with 10×10 trap stations at 10-m intervals[6,35]. There were two periods of 4–6 days, the first in June–July (phenological spring) and the second in August–September (phenologically autumn). All traps were checked daily. Lemmings were most frequently caught ($z_{mean} = 1.8$), but *Microtus oeconomus* ($z_{mean} = 0.45$), *Microtus agrestis* ($z_{mean} = 0.09$), *Sorex* ssp. ($z_{mean} = 0.10$), *Myodes glareolus* ($z_{mean} = 0.06$) and *Myodes rufocanus* ($z_{mean} = 0.02$) were also common. As preliminary analysis suggested that the Soricidae may respond somewhat atypically to the rest of the rodent group, probably owing to diet and metabolic rate differences as well as often being secondary prey relative to the rodents, they were not pooled with the non-lemming rodents and, hence, were not included in further analysis.

We also used the mean number of occupied passerine bird territories per square kilometre along three nearby transects and the number of occupied wader territories per square kilometre in the Finsefetene mudflats. These were gathered by repeated surveys[36,37] around the beginning of July 1967 until 1984 and 1985 for the waders and passerines, respectively. The data were pooled across species and transects.

The rodent trapping grids, the bird transects and mudflats and the Finse meteorological station all fit within an approximately 5×5-km^2 area to the south and east of the Finse railway station ($60.602°$ N, $7.504°$ E).

Hunter-recorded catches of ptarmigan (*Lagopus muta*) and willow grouse (*Lagopus lagopus*) were obtained from the Norwegian Bureau of Statistics (http://www.ssb.no). As there have been significant changes in reporting procedures and hunting behaviour that may induce low-frequency trends in the data, we use the logarithmic rate of change from one year to the next as the most reliable data, as well as a GAM-detrended version (these data transformations correlate closely ($r \approx 0.70$) and give qualitatively very similar results).

None of the logarithmic rates of change for the passerines, waders or ptarmigan and willow grouse showed significant temporal autocorrelation.

Climate and snow conditions. Here we use the extended winter NAO index of Hurrell[38,39] (December in year $t-1$ until March in year t), based on the difference between normalized sea-level pressure in Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland, together with meteorological records[40]. Also, snow data were sampled as part of winter-ecology courses held at Finse in March–April on 15 occasions during 1970–2008. These were organized by three of the authors (E.Ø., I.M. and T.S.), providing first-hand information on the average hardness, measured by penetrometers as the pressure (in kilograms per square centimetre) needed to make an indentation in the snow layer closest

to the ground[19]. Field estimates of the percentage of ground that is snow-covered around the 10th of July were also made every year during 1970–2000 by one of the authors (E.Ø.).

Using daily temperature maxima ($T_{i,t}^{\max, d}$) and minima ($T_{i,t}^{\min, d}$) we sum the constants θ_1 and θ_2, which represent the daily contributions to snow hardness (that is, the opposite of subnivean space formation), over the days i to find the temperature fluctuation impact $\bar{T}_t$ on snow hardness year t:

$$\bar{T}_t = \begin{cases} \sum_i T_{i,t}^{\max, d} - T_{i,t}^{\min, d} & \text{if } T_{i,t}^{\min, d} < -3,\ T_{i,t}^{\max, d} > 0 \\ \sum_i \theta_1 & \text{if } T_{i,t}^{\min, d} > -3,\ T_{i,t}^{\max, d} > 0 \\ \sum_i \theta_2 & \text{if } T_{i,t}^{\max, d} < 0 \end{cases} \quad (3)$$

Together with monthly averages of temperature maxima ($T_{j,t}^{\max, m}$), medians ($T_{j,t}^{\text{med, m}}$) and minima ($T_{j,t}^{\min, m}$) for month j, year t, this model was found to explain about 68% of the observed variance in mean measured hardness:

$$H_t = \exp\left(\theta_0 + f_3(\bar{T}_t) + f_4(T_{2,t}^{\text{med,m}} + T_{3,t}^{\max,m} + T_{4,t}^{\min,m} + T_{5,t}^{\min,m} + T_{10,t-1}^{\max,m})\right) + \varepsilon_t \quad (4)$$

The NAO, the precipitation in April in millimetres ($P_{4,t}$) together with monthly temperatures $\bar{T}_t' = T_{3,t}^{\text{med,m}} + c_3 T_{4,t}^{\text{med,m}} + T_{5,t}^{\text{med,m}}$ explain about 74% of the observed variance in median relative humidity in April (U_t):

$$U_t = \frac{100}{1 + \exp\left(-1(v_0 + v_1 \text{NAO}_t + v_2 \bar{T}_t' + v_3 P_{4,t} + v_4 P_{4,t} \bar{T}_t') + f_5(T_{4,t}^{\max,m} - T_{4,t}^{\min,m})\right) + \varepsilon_t} \quad (5)$$

The effects of NAO and temperature explain about 87% of the observed variance in July snow cover:

$$K_t' = \frac{100}{1 + \exp\left(-1(\kappa_0 + f_6(\text{NAO}_t) + f_7(T_{5,t}^{\max,m}) + f_8(T_{6,t}^{\max,m}) + f_9(T_{10,t-1}^{\max,m})\right) + \varepsilon_t} \quad (6)$$

Above, θ_0, κ_0 and $v_0, \ldots, v_4$ are estimated regression parameters, θ_1, θ_2 and c_3 are weighting constants. All parameters can be found in the Supplementary Information.

Simulations. As climatic fluctuations normally will prevent equilibrium states from being dominant, the transient dynamics are of ecological interest[4,31,41,42]. Hence, the dynamics captured by our population models were assessed through stochastic simulations (that is, using only the previous year's predicted population values when predicting the next, and adding random errors from the estimates distribution of the residuals). These were simulated over 100 yr for each of 10^3 different climate regimes generated by skewing their empirical probability distributions towards higher or lower values but not going beyond the observed range. The number of years between spring and/or autumn catch rates exceeding one lemming per 100 trap nights was adopted as a practical definition of cycle length.

31. Geritz, S. A. H. & Kisdi, E. On the mechanistic underpinning of discrete-time population models with complex dynamics. *J. Theor. Biol.* **228**, 261–269 (2004).
32. Rouyer, T., Fromentin, J.-M., Stenseth, N. C. & Cazelles, B. Analysing multiple time series and extending significance testing in wavelet analysis. *Mar. Ecol. Prog. Ser.* **359**, 11–23 (2008).
33. Cazelles, B. *et al.* Wavelet analysis of ecological time series. *Oecologia* **156**, 287–304 (2008).
34. Østbye, E. *et al.* Hardangervidda. *Ecol. Bull.* **20**, 225–264 (1975).
35. Stenseth, N. C. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* **87**, 427–461 (1999).
36. Østbye, E. *et al.* Structure and dynamics of some high mountain bird communities of South Norway: a 19-year study of passerines. *Ornis Norvegica* **25**, 19–48 (2002).
37. Østbye, E. *et al.* Structure and dynamics of a high mountain wetland bird community in southern Norway: An 18-year study of waders and gulls. *Ornis Norvegica* **30**, 4–20 (2007).
38. Hurrell, J. W. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* **269**, 676–679 (1995).
39. Stenseth, N. C. *et al.* Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. Lond. B* **270**, 2087–2096 (2003).
40. Norwegian Meteorological Institute. ⟨http://www.met.no⟩ (2008).
41. Schmidt, K. A. & Ostfeld, R. S. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. *Ecology* **89**, 635–646 (2008).
42. Dennis, B. *et al.* Can noise induce chaos? *Oikos* **102**, 329–339 (2003).