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*Research article*

# Macroecological patterns of rodent population dynamics shaped by bioclimatic gradients

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Long-term studies of cyclic rodent populations have contributed fundamentally to the development of population ecology. Pioneering rodent studies have shown macroecological patterns of population dynamics in relation to latitude and have inspired similar studies in several other taxa. Nevertheless, such studies have not been able to disentangle the role of different environmental variables in shaping the macroecological patterns. We collected rodent time-series from 26 locations spanning 10 latitudinal degrees in the tundra biome of Fennoscandia and assessed how population dynamics characteristics of the most prevalent species varied with latitude and environmental variables. While we found no relationship between latitude and population cycle peak interval, other characteristics of population dynamics showed latitudinal patterns. The environmental predictor variables provided insight into causes of these patterns, as 1) increased proportion of optimal habitat in the landscape led to higher density amplitudes in all species and 2) mid-winter climate variability lowered the amplitude in Norwegian lemmings and grey-sided voles. These results indicate that biome-scale climate and landscape change can be expected to have profound impacts on rodent population cycles and that the macro-ecology of such functionally important tundra ecosystem characteristics is likely to be subjected to transient dynamics.

Keywords: bioclimatic zones, climate, field vole, grey-sided vole, latitude, macroecology, Norwegian lemming, population dynamics, tundra ecosystem, tundra vole

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## Introduction

Studies of small rodents have contributed greatly to our understanding of population dynamics (Stenseth 1999, Berryman 2002, Turchin 2003). In particular, geographically distributed long-term series have provided opportunities for macroecological studies (Hansson and Henttonen 1985, Kendall et al. 1998, Boonstra and Krebs 2012, Cornulier et al. 2013, Ehrich et al. 2020). Such studies can reveal general patterns across large scales, enabling comparisons of climatic and other environmental drivers of population dynamics and ecosystem functioning (Blackburn 2004, Kerr et al. 2007). Notably, previous large-scale analyses of Fennoscandian rodents, which are renowned for their cyclic dynamics in boreal and arctic-alpine ecosystems, have shown strong latitudinal clines with longer population cycles and higher cycle peak densities in the north (Hansson and Henttonen 1988, Bjørnstad et al. 1995, Angerbjörn et al. 2001, Hanski et al. 2001, Korpela et al. 2013). This gradient and its suggested connection to a species richness gradient within the predator guild, i.e. higher diversity of predators in the south stabilizing rodent dynamics, has found its way into major ecology text books (Begon et al. 2006) and stimulated similar macroecological studies in other taxa (Kendall et al. 1998, Johnson et al. 2000, Murray 2000, Klemola et al. 2002, Post 2005, Sæther et al. 2008, Oliver et al. 2014).

In his book summarizing a century of research on rodent population dynamics, Charles Krebs (2013) proposed to compile quantitative time-series to test macroecological hypotheses as a research agenda for the next century. Such hypotheses can be based on knowledge from local and regional scale. For instance, at local scales population growth rates are higher in optimal habitats than elsewhere (Cockburn and Lidicker 1983, Bondrup-Nielsen 1987, Magnusson et al. 2015). Thus, at macroecological scales maximum population growth rates and consequently the highest amplitudes should be related to high proportions of optimal habitat in the landscape (Bondrup-Nielsen and Ims 1988, Lidicker and William 2000, Dalkvist et al. 2011). In terms of climate, freeze-thaw cycles can cause severe winter declines in arctic-alpine rodents (Kausrud et al. 2008, Hansen et al. 2013, Gauthier et al. 2024) limiting the population's potential to reach high abundances later during the summer and fall. Consequently, regions with more frequent mild spells can be expected to host rodent communities with lower and rounder population cycle peaks as compared to areas where cold winters and stable snow conditions are the norm. To test these macroecological hypotheses of population dynamics, a region where replicates of population dynamics time-series span different landscape and climatic contexts is essential (Buckley and Puy 2022). Fennoscandian tundra rodents are a suitable system for such study, as the tundra biome of the region extends across more than 10 latitudinal degrees and covers distinct climate and bioclimate gradients (Moen 1998, Virtanen et al. 2016), and time-series of rodent population dynamics are geographically widely distributed.

Although surrogate variables such as latitude and elevation may provide valuable clues about the underlying processes, more mechanistic variables are needed to reach beyond pattern description (Krebs 2013). Typically, several environmental variables change along latitudinal and elevational gradients, making their respective effects difficult to disentangle. Furthermore, previous studies on latitudinal gradients have merged data from different biomes such as natural and agricultural grassland, different forest biomes and tundra (Hanski et al. 1991, Bjørnstad et al. 1995, Tkadlec and Stenseth 2001, Boonstra and Krebs 2012). As rodent communities differ between biomes and are immersed in different food webs, the strength of different ecological interactions shaping population cycles are likely to differ. In particular, the Norwegian lemming *Lemmus lemmus*, the only rodent species endemic to the Fennoscandian tundra, has been observed to have higher and sharper population peaks than sympatric voles (Turchin et al. 2000, Ekerholm et al. 2001). Thus, the proportion of tundra – and consequently lemmings – can be an important determinant of regional rodent dynamics. The Norwegian lemming, as a tundra specialist, is also suggested to be more sensitive to a mild winter climate than other Fennoscandian rodent species (Kausrud et al. 2008, Ims et al. 2011). We propose that focusing on macroecological patterns of population dynamics within a single biome allows for stronger inferences owing to a more uniform species pool and less confounding between different potentially driving variables.

We first assessed whether biome-specific analyses of Fennoscandian rodents detected similar latitudinal patterns of the characteristics of population dynamics as previous studies. We focused on the tundra biome, where rodent cycles are prevalent and have a particularly strong impact on tundra food-web dynamics (Ims and Fuglei 2005). We then evaluated whether variables describing winter climate variability and landscape composition would give more insight to the observed patterns. We predicted that in locations with more variable winter climate the lemming makes up a smaller proportion of the rodent community and has lower density amplitude (hereafter amplitude). We further predicted that rodent species would both dominate the rodent community and reach the highest amplitudes in the parts of the tundra biome where their primary habitats occur.

## Material and methods

### Study system

The tundra biome covers the Arctic and oroarctic parts of Fennoscandia. Despite substantial variation in climate, the relatively simple food web has essentially a similar structure across the region. The low alpine bioclimatic zone is predominantly dwarf-shrub tundra and the middle alpine zone graminoid tundra (definitions according to Moen 1998; Supporting information). These tundra types have similar vegetation composition throughout the region, although the dwarf-shrub community has more arctic features in the north (Virtanen et al. 2016).

We focused on the four most abundant and widespread rodent species in the Fennoscandian tundra; the Norwegian lemming, the grey-sided vole *Myodes rufocanus* and two ecologically close *Microtus*-voles (*M. agrestis* and *M. oeconomus*, considered here as one functional group), and refer to them as genera. Based on food preferences (Soininen et al. 2013a), the low alpine zone contains optimum habitats for grey-sided voles. Lemmings, in turn, reach their highest numbers in the middle alpine zone (Ekerholm et al. 2001, Ims et al. 2011), which is dominated by their preferred food plants, i.e. graminoids and mosses (Soininen et al. 2013b). The *Microtus*-voles dwell in lush, moist, grass-rich habitats mainly found as patches in the low alpine zone (Hansson 1969, Henden et al. 2011).

## Time-series and spatiotemporal replication

We collected time-series from 26 different locations in the Fennoscandian tundra where lemmings occurred and where snap-trapping data on all species were available for ≥ 10 years (Table 1, Supporting information). Some of the locations also included trapping in adjacent ecotone forests (Supporting information). The time-series at the different locations had various degrees of spatial replication (sampling units such as quadrats or trap lines ranging from 1 to 74 per location; Table 1). To link rodent population dynamics with environmental variables, we focused on analyses at the sampling unit level as the area extent of locations ranged from < 1 to > 1000 km$^2$ (Supporting information). For details on inclusion/exclusion of locations and sampling units, see the Supporting information. In total, 22 locations ($n = 385$ sampling units) fulfilled all criteria.

We used data from the fall trapping season when available, as this is the season included in most data series (Table 1). We assume that fall data are more comparable between series than spring data, given that the varying match between the timing of spring trapping and phenology likely causes much noise in the data. For locations without fall trapping data, we used data from spring trapping season ($n = 3$ locations) or pooled data across variable trapping dates ($n = 4$ locations). To account for the effect of sampling seasons we 1) included sampling season as an additive factor in all regression models, and 2) tested whether excluding locations without fall data affected the results of the best models.

To make the time-series comparable, we used the number of rodents captured per 100 trap nights per sampling unit as an abundance index in all analyses.

The time-series included in this study were collected using snap-trapping, which is a standard method for monitoring tundra rodents traditionally used in the region. One reason for this is that snap trapping is the only trapping method that gives reliable data on Norwegian lemmings (Stenseth and Ims 1993). The main limitation of the snap-trapping index is that trappability differs among species, lemmings likely having lower trappability than voles. However, as our analyses were done species by species, interspecific differences in trappability should be less problematic. Moreover, we deem it unlikely that trappability of a species would change systematically across the targeted ecological gradients in the sense that it could bias our analyses. Another challenge for our analyses were the variable protocols employed for collection of the different time-series. We took several steps to make the data comparable, i.e. aggregating the data at a most comparable spatial scale (i.e. the sampling unit), including location identity in the analyses as a random factor, and analyses of aggregate measures of population dynamics. Thus, it is rather the precision of these estimates that may depend on the temporal and spatial extent of a locations' time-series, than the size of the estimates per se.

## Characteristics of rodent population dynamics

We focused on characteristics of rodent population dynamics that have consequences for ecosystem functioning, namely community contribution, mean density, amplitude, peak sharpness and peak interval. These characteristics and calculation of their indicators are presented in Table 2. We calculated the indicators per sampling unit and location, across the years when data was collected at that unit. The sampling units and locations thus represent spatial replicates of these indicators. We verified that our approach was not compromised by temporal trends (Supporting information).

Our focus was not to assess cyclicity of the rodent population dynamics, and many of the time-series were shorter than needed for formal statistical testing of cyclicity (e.g. by autoregressive models). However, our measure of amplitude (i.e. the s-index; Stenseth and Framstad 1980) has been found to be a useful indicator of cyclicity (Table 2, Henttonen et al. 1985).

## Environmental predictor variables

We derived environmental predictor variables from raster data. It was not a priori clear how large an area around a sampling unit best predicts the local rodent numbers. We therefore extracted environmental predictor variables at three spatial extents: 1, 9 and 25 km$^2$ around each sampling unit. Because the results differed only little, we present only results for the largest extent (25 km$^2$). We chose this extent because it had the highest number of locations where any sampling unit had any middle alpine zone within their buffers ($n = 3$, 8 and 9, at 1, 9 and 25 km$^2$, respectively). Results at other extents are given in the Supporting information.

To assess winter climate impact on rodent population dynamics, we extracted the long-term mean number of days in January–March when the daily mean temperature was above zero. An increase in the number of days with > 0°C would represent a more variable winter climate as the baseline is 0 or very low (i.e. stable 'winter climate'). This metric was available for the entire region and is linked to rodent winter demography (Aars and Ims 2002). We first created annual raster maps, depicting the number of days in January–March

Table 1. Description of small rodent snap-trapping time-series included in this study. The time-series in part (a) are included in all analyses, while the time-series in part (b) are only inlcuded in the location level analyses. For additional information on the complete time-series see the Supporting information. For all time-series in (a) we only included units that were active ≥ 10 years. Time-series numbers refer to Fig. 1. *=Trapped in other season than fall (spring or/and summer) or there are gaps in the time-series with inconsistent temporal and spatial trappings. **=Sometimes it varies between years which season that was trapped in.

(a)

| Location | Period | Sampling unit type | No. of sampling units year$^{-1}$ | Trap nights/ sampling unit | Trapping season (analysed season in bold) | Total no. of rodents (in the analysed data) | No. of rodents per 100 trap nights (in the analysed data) |
|---|---|---|---|---|---|---|---|
| 1. Nordkyn (NO) | 2004–2018 | Quadrate | 22 | 24 | Spring, **Fall** | 1571 | 19.96 |
| 2. Bekkarfjord (NO) | 2004–2018 | Quadrate | 16 | 24 | Spring, **Fall** | 1028 | 17.85 |
| 3. Stjernevann (NO) | 2004–2018 | Quadrate | 24 | 24 | Spring, **Fall** | 1472 | 17.04 |
| 4. Komagdalen (NO) | 2004–2018 | Quadrate | 14 | 24 | Spring, **Fall** | 843 | 16.73 |
| 5. Ifjordfjellet (NO) | 2004–2018 | Quadrate | 10 | 24 | Spring, **Fall** | 863 | 23.97 |
| 6. Vestre Jakobselv (NO) | 2004–2018 | Quadrate | 11 | 24 | Spring, **Fall** | 569 | 14.37 |
| 7. Joatka (NO) | 1986–2018 | Quadrate | 77 | 24 | Spring, **Fall** | 3422 | 7.66 |
| 9. Dividalen (NO) | 1993–2017 | Trap line | 5 | 300 | **Fall** | 343 | 0.91 |
| 10. Vassijaure (SE) | 1998–2018 | Quadrate | 10 | 24 | Spring, **Fall** | 444 | 8.81 |
| 11. Abisko (SE) | 1998–2018 | Quadrate | 10 | 24 | Spring, **Fall** | 355 | 7.04 |
| 12. Stora Sjöfallet (SE) | 2001–2018 | Trap line | 40 | 75–150 | Spring, **Fall** | 5388 | 5.71 |
| 13. Sørelva (NO)* | 2004–2018 | Quadrate | 9 | 24–36 | **Spring** | 56 | 1.36 |
| 14. Virvassdalen (NO)* | 2004–2018 | Quadrate | 9 | 24–36 | **Spring** | 101 | 2.28 |
| 16. Ammarnäs (SE) | 2001–2018 | Trap line | 44 | 50–150 | Spring, **Fall** | 9020 | 7.86 |
| 17. Øvre Elsvatn (NO)* | 2004–2016 | Quadrate | 9 | 24–36 | **Spring** | 66 | 1.78 |
| 18. Børgefjell 2 (NO)* | 2006–2018 | Quadrate | 40 | 12–24 | **Variable** | 256 | 4.40 |
| 19. Børgefjell (NO) | 1991–2015 | Trap line | 4 | 100 | **Fall** | 337 | 3.37 |
| 22. Vålådalen (SE) | 2001–2018 | Trap line | 42 | 60–150 | Spring, **Fall** | 6420 | 5.91 |
| 23. Åmotsdalen (NO) | 1991–2017 | Trap line | 4 | 50–150 | **Fall** | 638 | 5.83 |
| 24. Gutulia (NO) | 1993–2015 | Trap line | 4 | 100 | **Fall** | 167 | 1.82 |
| 25. Finse (NO) | 1970–2018 | 1 ha plot | 2 | 100–600 | Spring, **Fall** | 2274 | 3.99 |
| 26. Møsvatn (NO) | 1992–2017 | Trap line | 4 | 100 | **Fall** | 851 | 8.18 |

(b)

| Location | Period | Sampling type | No. of sampling units/year | Trap nights/ sampling unit | Trapping season (analysed season in bold)** | Total no. of rodents (in the analysed data) | No.of rodents per 100 trap nights (in the analysed data) |
|---|---|---|---|---|---|---|---|
| 8. Kilpisjärvi (FI)* | 1946–2012 (excl. 1948, 1976, 1984, 2010) | Trap line | 1–4 | ca 250 | Spring, **Fall** | 4448 | 12.80 |
| 15.Vindelfjällen (SE)* | 2001–2018 (excl. 2005, 2009, 2010, 2011, 2016) | Trap line | 2–12 | 60–360 | **Variable** | 106 | 0.75 |
| 20.Borgafjäll (SE)* | 2004–2016 (excl. 2009, 2010, 2014) | Trap line | 3–20 | 60–240 | **Variable** | 98 | 0.85 |
| 21. Helags (SE)* | 2001–2018 (excl. 2003, 2004, 2009, 2016) | Trap line | 2–42 | 60–360 | **Variable** | 616 | 2.85 |

with above-zero temperature. We chose this period because we expect snow-covered conditions throughout the study area. The annual maps were based on gridded daily mean temperature raster maps of Fennoscandia, available from the Norwegian Meteorological institute, Climatology Division (senorge.no). The daily maps are estimated by a residual interpolation approach, applying terrain and other predictor variables to define a trend that is removed from the observed temperatures before they are interpolated into a 1 × 1 km gridded field. The trend is then added to the interpolated field to obtain a spatially continuous gridded temperature map (Tveito et al. 2005). Based on the annual maps, we calculated a mean per sampling unit across a buffer zone (5 × 5 km) and the years when trapping was conducted at that unit.

To assess landscape composition, we used two approaches. First, we used a map of tundra bioclimatic zones in Norway (Moen 1998, Supporting information), published by Blumentrath and Hanssen (2010). The map is based on

Table 2. Rodent population dynamics characteristics and their indicators. Indicators were calculated per sampling unit across the years when data was collected at that unit. Data from fall trapping was used, except for three locations where only spring trapping was conducted (Table 1). For characteristics denoted with * the indicator was also calculated at location level.

| Characteristic | Functionality | Calculation of the indicator | Previously found latitudinal patterns in Fennoscandia | Resolution (community/ population) |
|---|---|---|---|---|
| Community contribution* | Different diets of voles and lemmings (Soininen et al. 2013a, b) lead to different effects on vegetation (Ravolainen et al. 2011). Lemmings strengthen alternative prey mechanism while voles do not (Ims et al. 2013) | Proportion of a given genus in the community, based on the total number of rodent individuals | None | Population. Each species contributes to the community with a species-specific proportion. Calculated for each rodent genus. See the Supporting information on calculation at location level |
| Mean density | Specialist predator population growth rate or population size increases with mean rodent density (Henden et al. 2008, Barraquand et al. 2014) | Mean trapping index | None | Community and population. Lemmings are a more important food source for some predators than voles (Killengreen et al. 2011, Ims et al. 2013). Calculated for each rodent genus |
| Density amplitude | Resource pulse magnitude modifies consumer response magnitude and lag to the pulse (Yang et al. 2010). Moss recovery decreases with increasing peak year disturbance (i.e. amplitude) (Rydgren et al. 2007). At low mean densities of rodents, predator population growth rate often increases with variability of rodent density (Henden et al. 2008, Barraquand and Yoccoz 2013) | Variability of the population abundance around the mean. Calculated using the standard deviation of log-transformed ($\log_{10}+0.01$) time-series, which is termed as the s-index, (Stenseth and Framstad 1980). S-indices > 0.5 indicate 3–5-year population cycles in rodents (Henttonen et al. 1985) | An increase from south to north (Hansson and Henttonen 1985, Hanski et al. 1991, Korpela et al. 2013) | Population. Expected to differ between species (Turchin et al. 2000). Calculated for each rodent genus |
| Peak sharpness | Resource pulse duration modifies consumer response duration and magnitude (Yang et al. 2010) | Based on skewness of the data, which is defined as $^{3}{}_{1} = \text{¼}_3 / \text{¼}_2^{3/2}$ ($\mu_2$ and $\mu_3$ are the second and third central moments of the time-series). Skewness describes the degree of asymmetry of data. Negative skewness relates to a few observations at very low density, but most near the maximum density (i.e. round cycles), whereas zero skewness relates to symmetric data and positive skewness to most observations at low density and only few at high densities (i.e. sharp cycles) (Turchin et al. 2000) | None | Population. Expected to differ between species (Turchin et al. 2000). Calculated for each rodent genus |
| Peak interval* | Moss recovery decreases with increasingly frequent cycles (Rydgren et al. 2007). Specialist predator growth rate increases with cycle frequency (Henden et al. 2008) | Mean number of years between population peaks. Year t was assigned as a peak year when a population had a positive growth rate from $t-1$ and negative to $t+1$. See Hanski et al. (1991) and the Supporting information | A decrease from south to north (Hansson and Henttonen 1985, Hanski et al. 1991, Bjørnstad et al. 1995) | Community. The species within community normally exhibit synchronous cycles, although lemmings sometimes skip peaks. Calculated for the entire rodent community, as different rodent species at the same location usually have synchronous cycles, and at sampling units with little data the signal of a cycle could be missed if evaluated for one species only |

modeling the tree-line elevation and thereafter estimating the elevation limits of the bioclimatic zones (Blumentrath and Hanssen 2010). The map has pixel size 25 × 25 m. For each sampling unit in Norway ($n = 221$), we extracted landscape composition by centering the sampling unit in the middle of a 25 $km^2$ (5 × 5 km) square and calculating the proportions of bioclimatic zones within the square. Second, we used July mean temperature (°C) as a proxy of bioclimatic zones, allowing inclusion of all locations ($n = 367$ sampling units). We used a temperature raster map of the July mean temperature for the normal period of 1981–2010, available from the Norwegian Meteorological institute, Climatology Division (Hanssen-Bauer et al. 2015). The map is based on a residual interpolation approach as described for the winter climate data. Within the bioclimatic zones, July mean temperature data was distributed as follows (mean °C ± SD): low alpine (10.6 ± 1.3), middle alpine (8.7 ± 1.5), and high alpine zone (6.8 ± 1.4) (Supporting information). To extract the July temperature variable for each sampling unit, we proceeded similarly as described for the winter climate data. As July mean temperature was less than 50% correlated with the variable describing winter climate variability ($rho = 0.41$), we proceeded to use both variables in common models.

### Statistical analyses of macroecological patterns in rodent population dynamics

We first assessed latitudinal patterns in the rodent population dynamics characteristics. At the level of sampling unit, we constructed a linear mixed effect model for each indicator for each rodent genus, with latitude and trapping season as fixed variables and location as a random variable. As location-level data has previously been used to assess latitudinal patterns (Hansson and Henttonen 1985, Bjørnstad et al. 1995), we also ran linear models of latitude impact on community contribution and peak interval using location-level data.

We then assessed the effect of environmental variables on the indicators, focusing on community contribution and amplitude (Fig. 2). We constructed two model sets: 1) model set for all data ($n = 385$ sampling units from 22 locations) using July temperature and winter climate variability as predictor variables, and 2) model set for Norwegian data ($n = 239$ sampling units from 17 locations) using the proportion of optimal bioclimatic zone (low alpine for voles and middle alpine for lemmings) as predictor variable instead of July temperature. For each rodent genus and both model sets, we included all additive combinations of relevant predictor variables, together with trapping season as a fixed variable and location as a random variable. Visual inspection of the data indicated a non-linear effect of summer temperature for the two vole genera (i.e. temperature optimum, Fig. 3), and we therefore included a quadratic term of temperature in these models. In all models for community contribution, we log-transformed the response variable to achieve close to normal distribution.

We assessed if, despite the large-scale synchrony in the occurrence of rodent population peaks, there was spatial autocorrelation in the indicators beyond the extent of location. To do this, we assessed the evidence for a spatial autocorrelation of the predicted random effects for location (Supporting information). When there was evidence for such autocorrelation, it could be removed by including latitude as an additional covariate, and we checked if results were robust to the inclusion of latitude as a covariate (Supporting information). We selected the best models in each candidate model set based on $AICc_c$ (Burnham and Anderson 2002). Model selection was run with and without latitude as a covariate when there was evidence for spatial autocorrelation.

All data analyses were done in the software R ver. 4.0.3 (www.r-project.org) using packages ‘lme4’ (linear mixed effect models, Bates et al. 2008), ‘AICcmodavg’ (AICc based model selection, Mazerolle 2012), and ‘raster’ (extracting climate data, Hijmans and Etten 2012). We used 95% confidence intervals to measure uncertainty for effects, and inspected model fit to assumptions using diagnostic plots.

## Results

### Indicators of rodent population dynamics

At the sampling unit level, the community contributions of all three rodents ranged from 0–100% (Supporting information). However, lemmings and *Microtus* were abundant in only few locations. The median of community contribution across sampling units was > 50% in two locations for lemmings and in three locations for *Microtus*, while the same was true for ten locations for grey-sided voles. At the location level, community contribution of grey-sided voles and lemmings ranged from almost absence (1–3%) to complete dominance (80–88%), while *Microtus* reached at most 57% community contribution (Fig. 1b, Supporting information).

Peak interval ranged from 2 to 13 years at the sampling unit level. The very long maximum intervals arose from sampling units where a peak was absent despite being present at other sampling units within the same location. Consequently, peak intervals at sampling unit scale which were longer than twice the mean across all units (i.e. > 8 years) were removed from the analyses. This resulted in a peak interval range from 2.0 to 6.8 (mean 3.8 years; Supporting information). Peak interval was less variable at the location level than at the sampling unit level (ranging from 3.2 to 4.7 with a mean of 3.9, Supporting information).

At the sampling unit level, mean density was the indicator with clearest differences between the rodent genera (Fig. 2, see the Supporting information for all values in this paragraph and the associated measures of uncertainty). Grey-sided voles mean densities were on average higher than those of lemmings and *Microtus* (mean across all sampling units: 1.3, 5.3 and 2.6 for lemmings, grey-sided voles and *Microtus*, respectively). Grey-sided voles also had the highest sampling unit specific mean densities, respectively two and five times higher than for lemmings and *Microtus*. Amplitudes varied less, although the mean across lemming amplitudes was

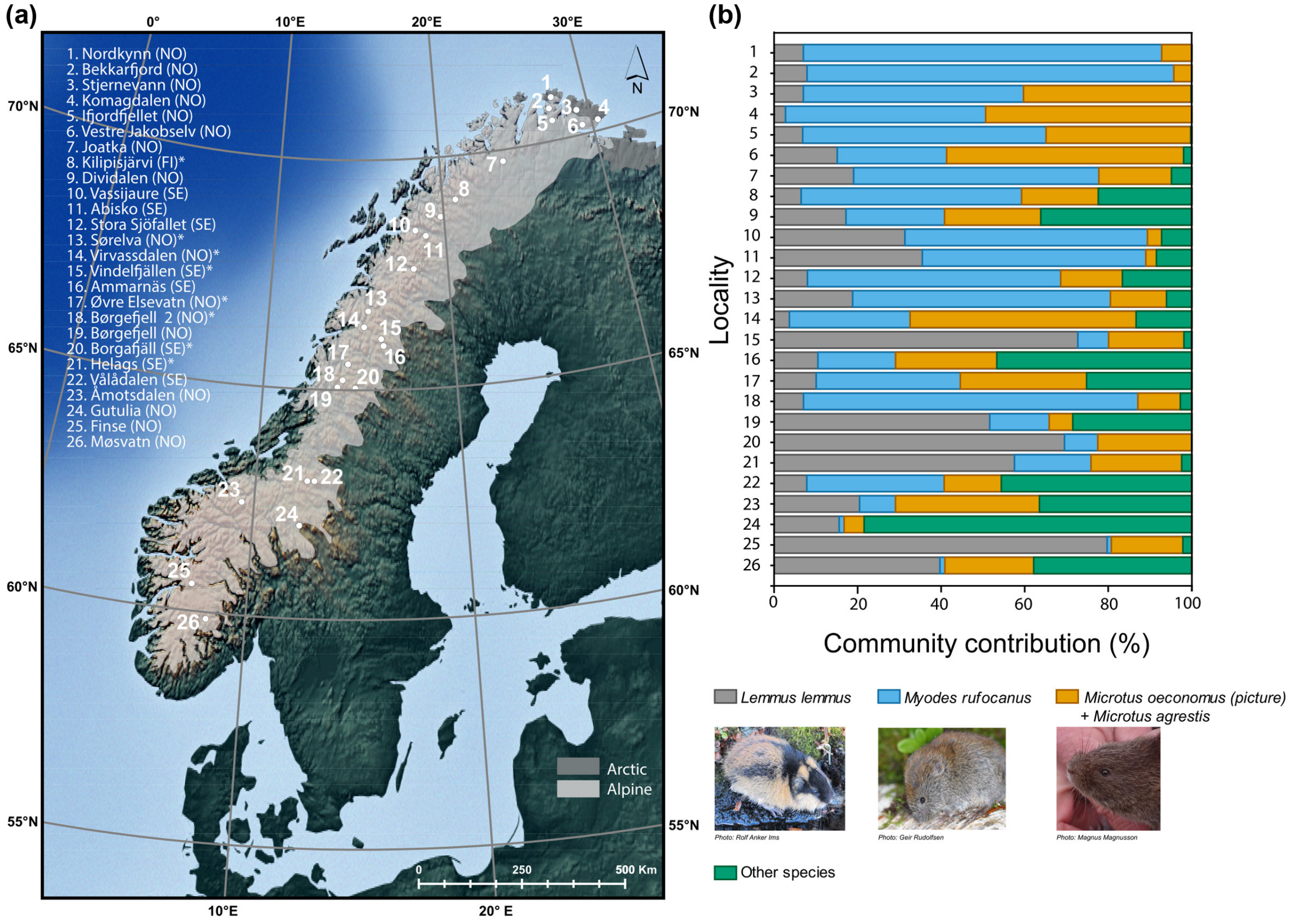

Figure 1. (a) Study areas (n = 26 locations) located in the alpine and Arctic regions of Fennoscandia in northern Europe where small rodents have been snap-trapped in fall ≥ 10 consecutive years. Locations denoted with * are exceptions (trapping conducted only in spring or/and summer or with gaps in the respective time-series; see details in Table 1). (b) Community contribution of rodent genera within each location during this study: the grey-sided vole *Myodes rufocanus* (blue bars); Norwegian lemming *Lemmus lemmus* (grey bars); field vole *Microtus agrestis* and tundra vole *Microtus oeconomus* (the last two combined as *Microtus*-species; orange bars); and other species (green bars) encompassing the bank vole *Myodes glareolus,* red-backed vole *Myodes rutilus* and wood lemming *Myopus schisticolor*.

slightly lower than those of voles (s-index 1.0, 1.2 and 1.1 for lemmings, grey-sided voles and *Microtus*, respectively). The majority of sites had amplitude/s-index above 0.5 for all species, indicating cyclic dynamics (98% for lemmings and 96% for both voles). In contrast, the mean across lemming skewness was higher than those of voles (1.9, 0.5 and 1.3 for lemmings, grey-sided voles and *Microtus*, respectively). This indicates that lemming peaks were on average lower and sharper than vole peaks.

The indicators were connected in all species in a similar manner (Supporting information). High community contribution, high mean density, high amplitude and low (below-zero or zero) skewness tended to occur together, as did low community contribution, low mean density, low amplitude and high (above-zero) skewness (Supporting information). This indicates that independent of species identity, the dominant species in the rodent community had high and round population peaks, whereas lower and sharper peaks characterized less abundant species. However, lemming skewness always remained above-zero (Fig. 2, Supporting information), indicating that sharp peaks were a consistent characteristic of this species.

## Latitudinal patterns of population dynamics

The relationship to latitude differed between species (Fig. 2, Table 3). Based on sampling unit specific analyses, the lemming community contribution decreased northwards, but the other lemming characteristics showed no latitudinal patterns. Grey-sided voles' community contribution increased northwards, as did their mean density and amplitude, whereas their peak skewness decreased (i.e. peaks were less sharp). Also, *Microtus*' mean density and amplitude increased northwards, but less strongly than those of grey-sided voles (Fig. 2, Table 3). The mean density of the rodent community (i.e. all species combined) increased northwards, but we found no latitudinal patterns in peak interval. Location level patterns of community contribution were similar to patterns at sampling unit level (Supporting information). Location level peak interval had no clear latitudinal trends, either. We

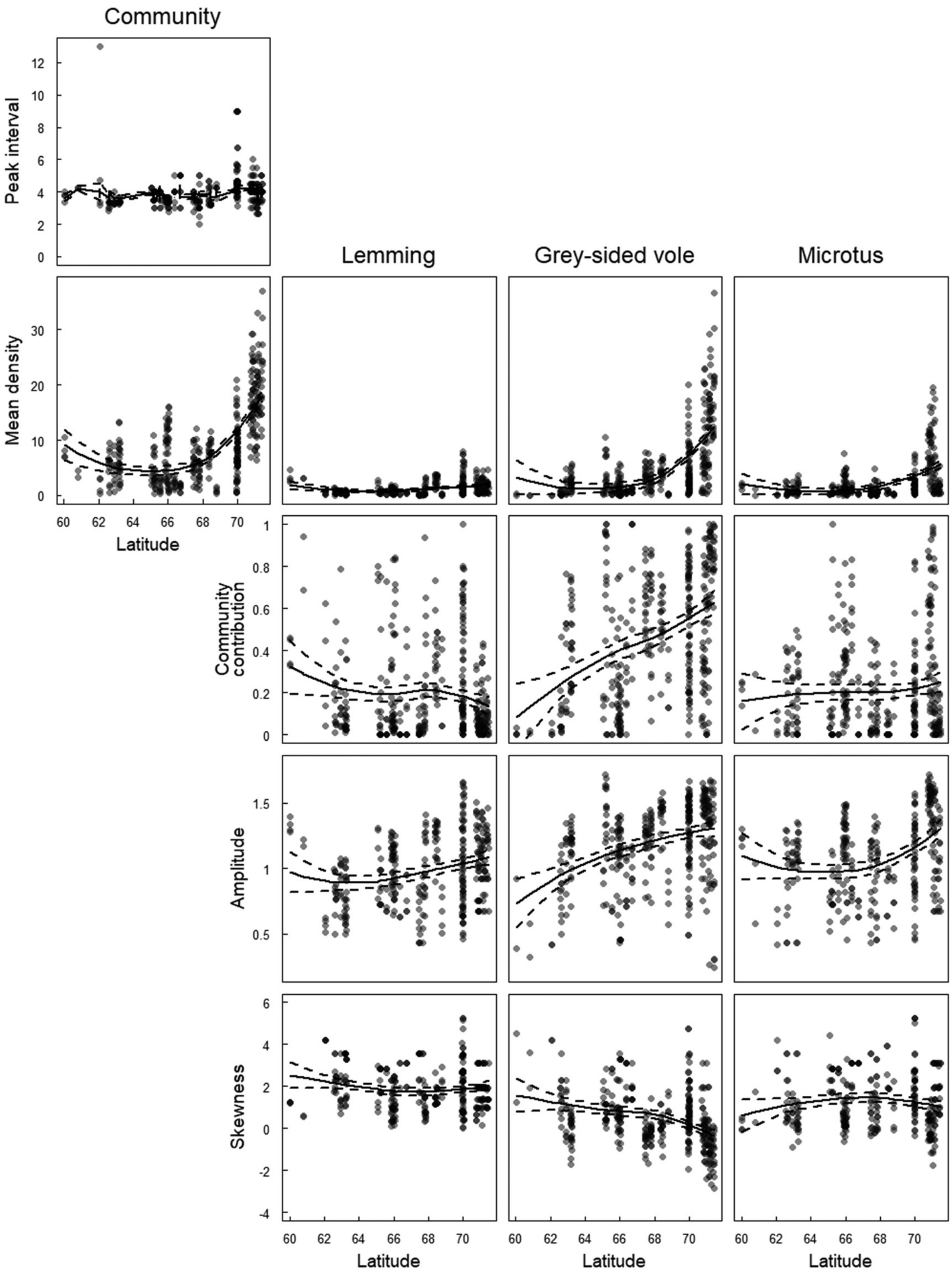

Figure 2. Relationships between latitude and characteristics of small rodent population dynamics in the small rodent community of Fennoscandian tundra, based on time-series from 385 sampling units from 22 locations (Table 1a). The plots for peak interval and community contribution include all sampling units. The plots for mean density, amplitude and skewness include only the sampling units where a given genus was present (n = 334, 367, and 305 for lemmings, grey-sided voles and *Microtus*, respectively). For definitions of population dynamics characteristics variables see Table 2. Lines show fitted values from a loess-smoother (solid lines) and its 95% confidence intervals (dashed lines).

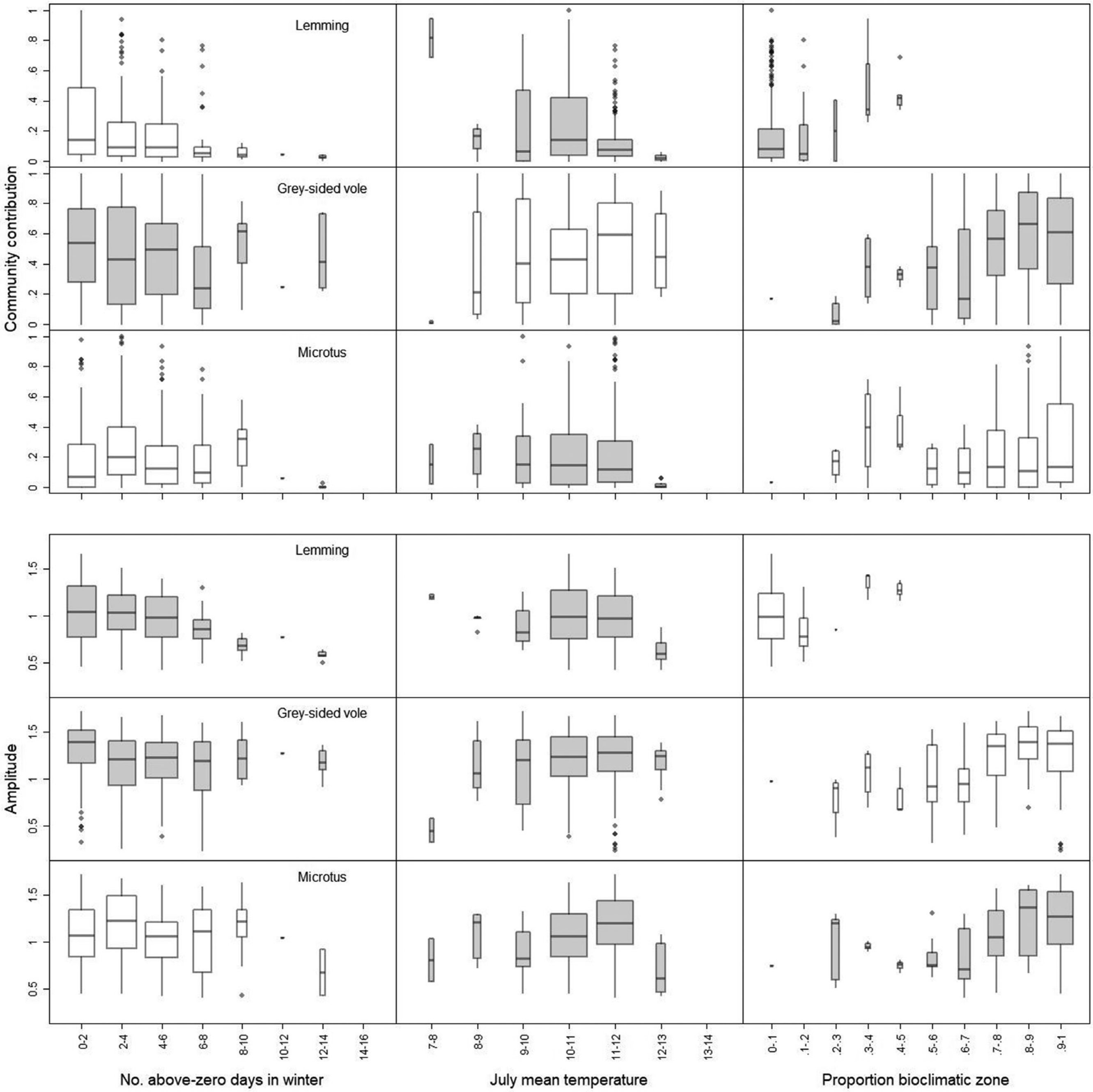

Figure 3. Relationship between environmental predictor variables and characteristics of small rodent population dynamics of Fennoscandian tundra, based on time-series from 385 sampling units from 22 locations (Table 1a). The panels for number of above-zero days in winter and July mean temperature include data from all locations, while the panels for bioclimatic zone include data from the Norwegian locations only (n = 17). Proportion of bioclimatic zone refers to the presumed optimal bioclimatic zone of each rodent genus (low alpine zone for voles, middle alpine zone for lemmings). The plots for community contribution include all available sampling units (n = 385 for winter climate and July temperature, 239 for bioclimatic zones). The plots for amplitude include only the sampling units where a given species was present (n = 334, 367, and 305 [lemmings, grey-sided voles and *Microtus*] for winter climate and July temperature, n = 194, 225, and 181 [lemmings, grey-sided voles and *Microtus*] for bioclimatic zones). Width of boxes is proportional to the number of observations. Horizontal line shows median, boxes the 50% interquartile range, whiskers minimum and maximum, and points outliers. Environmental variables were calculated across a 25 km$^2$ buffer zone, for figures with 9 and 1 km$^2$ buffers (Supporting information). Grey boxes indicate variables that were statistically significant in the best models in either model set (Table 4).

Table 3. Model results for latitude effects on characteristics of rodent population dynamics. Values in parentheses show 95% confidence limits; predictor variable estimates for which the 95% confidence intervals do not cross zero are denoted in bold. Random effects are given as standard deviation of variation; in parentheses is the proportion of variance assigned to location effect. Stars denote effects of latitude that were statistically significant when data from fall only was included in the models. Unit of latitude is 100 km; the effect size estimate corresponding to a 100 km northwards movement. In all models for community contribution, we log-transformed the response variable to achieve close to normal distribution. Reference level for the factorial variable sampling season is fall; the effect size estimate corresponds to a difference between fall and spring. The community-level models and models for community contribution include all available sampling units, while the other models include only the sampling units where the target genus was present, sample size given in parenthesis.

| Response variable | | Model estimates | | | | |
|---|---|---|---|---|---|---|
| | | Intercept | Fixed effects | | Random effects | |
| | | | Latitude | Sampling season (spring) | Location (n=22) | Residual |
| Community | Mean density (n=385) | −74.72 (−111.30, −38.26) | **1.13 (0.64, 1.62)*** | **−6.64 (−12.12, −1.16)** | 4.39 (0.53) | 4.14 |
| | Peak interval (n=373) | 1.20 (−1.79, 4.20) | 0.04 (−0.01, 0.07) | −0.26 (−0.26 0.61) | 0.31 (0.27) | 0.52 |
| Lemming | Community contribution (n=385) | 5.36 (−0.92, 11.67) | **−0.10 (−0.18, −0.02)*** | **−1.32 (−2.24, −0.41)** | 0.66 (0.24) | 1.16 |
| | Mean density (n=334) | 0.41 (−6.64, 7.51) | 0.01 (−0.08, 0.11) | −1.06 (−2.20, 0.07) | 0.76 (0.30) | 1.16 |
| | Amplitude (n=334) | 0.28 (−1.22, 1.79) | 0.01 (−0.01, 0.03) | **−0.25 (−0.49, −0.01)** | 0.17 (0.34) | 0.23 |
| | Skewness (n=334) | 3.58 (−1.66, 8.82) | −0.02 (−0.09, 0.05) | 0.80 (−0.05, 1.65) | 0.56 (0.27) | 0.92 |
| Grey-sided vole | Community contribution (n=385) | −19.00 (−25.01, −13.03) | **0.23 (0.16, 0.32)*** | 0.44 (−0.42, 1.31) | 0.66 (0.34) | 0.92 |
| | Mean density (n=367) | −71.35 (−101.81, −40.89) | **1.03 (0.62, 1.43)*** | −3.18 (−7.61, 1.24) | 3.41 (0.42) | 4.01 |
| | Amplitude (n=367) | −2.78 (−4.44, −1.12) | **0.05 (0.03, 0.07)*** | −0.12 (−0.35, 0.11) | 0.17 (0.30) | 0.26 |
| | Skewness (n=367) | 18.79 (12.16, 25.45) | **−0.24 (−0.33, −0.16)*** | **1.07 (0.14, 2.00)** | 0.68 (0.30) | 1.01 |
| *Microtus* | Community contribution (n=385) | −3.11 (−11.99, 5.76) | 0.01 (−0.11, 0.13) | 0.38 (−0.94, 1.69) | 1.02 (0.41) | 1.23 |
| | Mean density (n=305) | −26.17 (−45.68, −6.59) | **0.39 (0.12, 0.65)*** | −1.40 (−4.34, 1.55) | 2.26 (0.45) | 2.51 |
| | Amplitude (n=305) | −1.33 (−3.35, 0.68) | **0.03 (0.01, 0.06)*** | −0.21 (−0.51, 0.10) | 0.24 (0.49) | 0.24 |
| | Skewness (n=305) | 3.78 (−4.20, 11.78) | −0.03 (−0.14, 0.07) | **1.38 (0.18, 2.59)** | 0.93 (0.45) | 1.03 |

explored visually patterns between peak interval and other variables (location, environmental variables; Supporting information), but found no patterns.

## Effects of climate and landscape on population dynamics

The mean number of days with above-zero temperatures during January–March ranged from 0.9 to 13.9 days per sampling unit, while July mean temperature ranged from 7.6 to 12.7°C (for all values in this paragraph see Supporting information). Among the Norwegian locations where we had data for alpine bioclimatic zones, low alpine tundra dominated independent of spatial scale. Within a 25 $km^2$ neighborhood, low alpine zone made up an average of 81% (range 8–99%), while mid alpine zone made up just 3% (range 0–43%). Furthermore, only 9 out of 17 Norwegian locations had sampling units with any middle alpine zone within their buffers, while low alpine zone was present at all locations. All variables were correlated with latitude; the correlation was positive for July temperature and low alpine tundra, and negative for the other variables (Supporting information).

For lemmings, high community contribution and high amplitudes were related to the colder parts of the landscape (Table 4, Fig. 3 for this and subsequent paragraphs). The model set with all data indicated a negative effect of July temperature on both aspects of the species population dynamics. The model set with only Norwegian data supported this by indicating a positive effect of middle alpine zone on community contribution. Winter climate variability was not included in the best models for lemming community contribution, but it had a negative effect on lemming amplitude.

For grey-sided voles, the different model sets indicated different effects. The model set for all data related community contribution positively to winter climate variability and amplitude positively to July temperature. In contrast, the model set for only Norwegian data related community contribution negatively to the optimal bioclimatic zone and amplitude negatively to winter climate variability.

The *Microtus* community contribution was related to the surrounding landscape. The model set for all data indicated a negative effect of July temperature, while the model set with only Norwegian data indicated a positive effect of the proportion of low alpine zone. The results for *Microtus* amplitude indicated a negative effect of high July temperatures and a positive effect of the proportion of the low alpine zone. Winter climate was not included in any of the best models for *Microtus*. However, it was included in the second-best models, and in the best models for amplitude at the most local scale (Supporting information).

## Discussion

Our study is the first biome-specific macroecological analysis of a rodent community at the scale of a biogeographic region. Interestingly, we found no evidence for the previously found

Table 4. Model results for winter climate variability (mean number of above-zero days during January–March), July mean temperature, and bioclimatic zones (proportion of presumed optimal bioclimatic zone of the surrounding 25 km$^2$ landscape) on characteristics of rodent population dynamics. The models for community contribution (abbreviated as 'community cont.') include all available sampling units, while the models for amplitude include only the sampling units where a given genus was present, sample size given in parenthesis. For voles, the presumed optimal bioclimatic zone is the low alpine zone, for lemming the middle alpine zone. Results for best models are shown, dataset A refers to 'all data' (n = 22 locations), dataset N to 'Norwegian data only' (n = 17 locations). Values in parentheses show 95% confidence limits; predictor variable estimates for which the 95% confidence interval does not cross zero are denoted in bold. Random effects are given as standard deviation of variation; in parentheses is the proportion of variance assigned to location effect. Star denotes effects that were statistically significant when data from fall only was included in the models. Dash denotes variables that were included in the set of evaluated models, but did not appear in the best model, whereas empty cells denote variables that were not evaluated in the given model set. Reference level for the factorial variable sampling season is fall; the effect size estimate corresponds to a difference between fall and spring. See the Supporting information for model selection table and results at 9 and 1 km$^2$.

| | | Intercept | Fixed effects | | | | | Random effects | |
|---|---|---|---|---|---|---|---|---|---|
| Response variable (dataset, sample size) | | | Winter climate variability | July temperature | July temperature$^2$ | Optimal bioclimatic zone | Sampling season (spring) | Location | Residual |
| Lemming | Community cont. (A, n = 385) | 5.96 (3.64, 8.12) | – | **−0.75 (−0.94, −0.53)*** | | | **−1.36 (−2.46, −0.26)** | 0.84 (0.37) | 1.08 |
| | Community cont. (N, n = 239) | −2.47 (−2.92, −2.01) | – | | | **4.47 (2.87, 6.73)*** | −0.85 (−1.88, 0.16) | 0.72 (0.27) | 1.18 |
| | Amplitude (A, n = 334) | 2.56 (2.05, 30.04) | – | **−0.14 (−0.19, −0.10)*** | | | **−0.29 (−0.57, −0.001)** | 0.21 (0.22) | 0.50 |
| | Amplitude (N, n = 194) | 1.22 (1.05,1.38) | **−0.06 (−0.09, −0.02)*** | | | – | −0.21 (−0.46, 0.05) | 0.17 (0.32) | 0.25 |
| Grey-sided vole | Community cont. (A, n = 385) | −2.03 (−2.65, −1.43) | **0.12 (0.05, 0.19)*** | – | – | | 0.15 (−1.29, 1.60) | 1.15 (0.62) | 0.91 |
| | Community cont. (N, n = 239) | −0.35 (−1.70,0.92) | – | | | **−1.83 (−3.13, −0.22)** | 0.15 (−1.81, 2.11) | 1.55 (0.74) | 0.93 |
| | Amplitude (A, n = 367) | 0.38 (−0.17, 0.93) | – | **0.07 (0.02, 0.12)*** | – | | −0.18 (−0.48, 0.13) | 0.24 (0.45) | 0.26 |
| | Amplitude (N, n = 225) | 1.29 (1.07, 1.52) | **−0.05 (−0.09, −0.01)** | | | – | −0.09 (−0.45, 0.29) | 0.28 (0.51) | 0.28 |
| *Microtus* | Community cont. (A, n = 385) | −2.13 (−2.67, −1.59) | – | −2.76 (−6.24, 0.54)* | **−7.07 (−10.38, −3.53)*** | | −0.03 (−1.48, 1.40) | 1.13 (0.48) | 1.18 |
| | Community cont. (N, n = 239) | −2.93 (−4.20, −1.64) | – | | | 1.15 (−0.39, 2.64) | 0.33 (−1.03, 1.69) | 1.00 (0.37) | 1.29 |
| | Amplitude (A, n = 305) | 1.10 (0.97, 0.32) | – | 0.32 (−0.36, 0.99) | **−1.01 (−1.70, −0.29)*** | | −0.30 (−0.64, 0.04) | 0.27 (0.55) | 0.24 |
| | Amplitude (N, n = 181) | 0.72 (0.44, 1.00) | – | | | **0.52 (0.20, 0.84)*** | −0.20 (−0.54, 0.14) | 0.26 (0.57) | 0.23 |

northwards increasing peak interval (Bjørnstad et al. 1995, Hanski et al. 2001), even though a similar gradient in amplitude was present in parts of the rodent community. The rodent community characteristics were related to landscape composition, indicating that bioclimatic zonation is a more informative predictor of structure and functioning of tundra rodent communities than latitude. Furthermore, increasing winter climate variability decreased amplitudes of both lemmings and grey-sided voles, implying that impacts of a warming winter climate may not necessarily be divergent between lemmings and voles as we hypothesized. Taken together, environmental variables provided new understanding beyond latitudinal patterns.

Our results matched only partly the earlier macroecological descriptions of Fennoscandian rodent population dynamics (Hansson and Henttonen 1988, Hanski et al. 1991, Bjørnstad et al. 1995, Angerbjörn et al. 2001, Korpela et al. 2013). The overall patterns in peak intervals and amplitude (i.e. the s-index) corresponded to 3–5-year population cycles that are a norm for the region. However, we found no support for the latitudinal gradient in rodent population peak interval, and only species-specific gradients in amplitude, mean density, skewness, and community contribution. This could indicate that the previously observed patterns arise from comparisons between biomes (e.g. less variable peak intervals in the tundra than in the boreal biome) and/or from pooling of different species. Furthermore, it is unlikely that peak interval remains fixed over several decades. Our findings thus support the conclusion of Henden et al. (2009); that the Fennoscandian latitudinal gradient of small rodent population dynamics is not a temporally persistent phenomenon and may rather be a case of transient dynamics (Hastings et al. 2018). Hence, macro-ecological studies of population dynamics need to consider appropriate temporal and spatial study extents (Wiens 1989). While latitudinal gradients of population dynamics beyond Fennoscandian rodents have been observed in some regions and species (rodents: Saitoh et al. 1998, Erb et al. 2000, Tkadlec and Stenseth 2001; ungulates: Post 2005; ducks: Sæther et al. 2008; butterflies: Oliver et al. 2014), but not in others (rodents: Boonstra and Krebs 2012), we encourage future studies to assess biome- and species-specific patterns at appropriate spatio-temporal study extents.

We found that a mild winter climate – as an indicator of less stable snow conditions – decreased the amplitude of both lemmings and grey-sided voles, while the community contribution of grey-sided voles increased. Thus, our analyses did not support the hypothesized dichotomy of winter climate impact on lemmings versus voles. We did, however, find less evidence for an effect of winter climate on *Microtus*-voles than for the other species, although this result must be interpreted with caution. As *Microtus* were scarce in most locations (n = 2 locations with more than 50% *Microtus*), our ability to detect strong patterns may have been reduced. Moreover, although within-year spring and fall abundances are usually well correlated (Kausrud et al. 2008, Cornulier et al. 2013), winter climate is expected to have the most direct impact on spring abundances. In any case, our study highlights that snow quality likely affects functioning of the entire below-snow community, as also indicated by Scott et al. (2022).

Our results show that lower cycle amplitudes are associated with milder winters. This is partly in line with Fennoscandian local-scale studies (Ruffino et al. (2016), but see Andreassen et al. (2020) for a difference between voles and lemmings). Few studies outside Fennoscandia have directly addressed the relationship between cycle amplitude and winter climate. Yet, a recent macroecological circumarctic study (Gauthier et al. 2024) and local-scale studies from arctic (Domine et al. 2018), boreal (Schmidt et al. 2018), and temperate (Jolly et al. 2024) regions indicate that unstable, non-insulating, and icy snowpack is linked to lower rodent abundances and winter growth rates. Still, not all studies find support for such winter climate impacts (Gouveia et al. 2015, Krebs et al. 2019), and other climate change impacts on amplitude, linking longer and warmer growing seasons with increased food availability have also been proposed (Schmidt et al. 2018). Given the variable climate and snow regimes across the northern hemisphere, coupled with different extent of changes, it is unsurprising that different studies find different effects of winter climate on rodent cycles. Macroecological study designs covering gradients of variable snow conditions are essential to disentangle such context dependencies. However, their impact could be vastly improved if they combined locally measured data on snow structure to acquire more mechanistic variables (Kausrud et al. 2008, Domine et al. 2018, Scott et al. 2022) rather than the proxies currently available (this study, Gauthier et al. 2024). Given the climate-change driven changes of snow conditions (Pall et al. 2019) and the key role of rodents in tundra food webs (Ims and Fuglei 2005), we encourage future studies to probe into the mechanisms of snow condition impacts on rodent population dynamics.

We found support for our hypothesis that higher community contribution and amplitudes are attained in landscapes with a higher proportion of optimal habitat for a given species. Our findings are thus in line with empirical smaller-scale studies and theoretical studies supporting the idea that landscape structure is an important determinant of both rodent community structure (Cavia et al. 2009, Ecke et al. 2017) and species-specific population dynamics (Bondrup-Nielsen and Ims 1988, Delattre et al. 1999, Lidicker and William 2000, Magnusson et al. 2015). However, some of the observed patterns appeared contradictory, notably for *Microtus* where models using bioclimatic zonation as predictor showed hypothesized patterns whereas models using July temperature as predictor indicated the opposite. This may be related both to *Microtus* being scarce in most locations and to contrasting validity of the two predictors as a proxy for habitat quality. The latter may be resolved by developing improved environmental predictor variables with a stronger mechanistic link to local species-specific vital rates.

## Future perspectives

We propose that the Fennoscandian tundra and its rodent community are well suited for further biome-specific macroecological studies. The variation in climate and bioclimatic conditions, together with widely distributed population dynamics time-series, enables structured macroecological study designs (Buckley and Puy 2022). We here show that the rodent population dynamics characteristics of this region vary greatly within the biome and between the rodent genera. More focused assessments of causes of such variation have been called for (Krebs 2013, Myers 2018), as most previous studies have been restricted to a few locations and local context dependencies are therefore almost unknown (cf. Soininen et al. 2018). The tundra biome is the terrestrial biome on Earth most affected by climate change (Post et al. 2009, CAFF 2013, Box et al. 2019) and the existing spatial configuration of population dynamics is likely to change accordingly. Macroecological monitoring of the tundra biomes' key players is a valuable approach to detect the impacts of climate change on tundra ecosystem functioning.

Yet, we see considerable scope for improvements for future macroecological studies on small rodent population dynamics – in Fennoscandia and elsewhere. Harmonization of practices through implementation of a common camera trapping design (Kleiven et al. 2022) enables year-round monitoring with similar detectability between species (Mölle et al. 2021). Yet, live- and snap-trapping provide samples that are crucial for macroecological questions related to for example ecotoxicology (Ecke et al. 2020), genetics (Hope et al. 2023), and disease ecology (Niklasson et al. 1995, Khalil et al. 2016, Sipari et al. 2022). A more balanced representation of bioclimatic zones would provide a better case for relating each species to their optimal parts of the landscape. Better insight may further be achieved by development of environmental predictor data layers across country borders, and development of more mechanistic predictor variables of climate. This recommendation appears to be equally relevant for macroecological studies of population dynamics within other taxa, which often fail to unambiguously relate patterns to underlying drivers (Klemola et al. 2002, Fuglei et al. 2020).

Long-term data in ecology is important in the face of anthropogenic driven changes of land-use, climate, and contaminant loads (Berteaux et al. 2017, Ims and Yoccoz 2017, Ecke et al. 2020). The scientific community has recognized its importance (Lindenmayer et al. 2012, Haase et al. 2016), but consistent funding remains a challenge (Callaway et al. 2012). Yet, continued funding and increased coordination are prerequisites to achieve an efficient macroecological study design.

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*Permits* – The data for this manuscript has been collected from three countries and several long-term monitoring initiatives from different institutions. These have operated according to the respective national regulations and ethics guidelines of the respective institutions.

## Author contributions

**Eeva M. Soininen**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Magnus Magnusson**: Data curation (lead); Formal analysis (supporting); Funding acquisition (equal); Visualization (equal); Writing – review and editing (supporting). **Jane U. Jepsen**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Writing – review and editing (supporting). **Nina E. Eide**: Conceptualization (equal); Data curation (lead); Funding acquisition (equal); Methodology (equal); Writing – review and editing (supporting). **Nigel G. Yoccoz**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – review and editing (supporting). **Anders Angerbjörn**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Jo Inge Breisjøberget**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Frauke Ecke**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Dorothee Ehrich**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Erik Framstad**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Heikki Henttonen**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Birger Hörnfeldt**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Siw Killengren**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Johan Olofsson**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Lauri Oksanen**: Data curation (supporting); Funding acquisition (equal); Investigation (equal); Writing – review and editing (supporting). **Tarja Oksanen**: Data curation (supporting); Funding acquisition (equal); Investigation (equal);

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### Transparent peer review

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### Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h9w0vt4t6. (Soininen et al. 2024).

### Supporting information

The Supporting information associated with this article is available with the online version.

## References

Aars, J. and Ims, R. A. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. – Ecology 83: 3449–3456.

Andreassen, H. P., Johnsen, K., Joncour, B., Neby, M. and Odden, M. 2020. Seasonality shapes the amplitude of vole population dynamics rather than generalist predators. – Oikos 129: 117–123.

Angerbjörn, A., Tannerfeldt, M. and Lundberg, H. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. – Ecography 24: 298–308.

Barraquand, F. and Yoccoz, N. G. 2013. When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. – Theor. Popul. Biol. 89: 1–11.

Barraquand, F., Høye, T. T., Henden, J. A., Yoccoz, N. G., Gilg, O., Schmidt, N. M., Sittler, B. and Ims, R. A. 2014. Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and Arctic lemmings. – J. Anim. Ecol. 83: 375–387.

Bates, D., Maechler, M. and Dai, B. 2008. lme4: linear mixed-effects models using s4 classes (ver. 0.999375-37). – https://CRAN.R-project.org/package=lme4

Begon, M., Townsend, C. R. and Harper, J. L. 2006. Ecology, from individuals to ecosystems. – Blackwell Publishing.

Berryman, A. A. 2002. Population cycles: the case of trophic interactions. – Oxford Univ. Press.

Berteaux, D. et al. 2017. Harmonizing circumpolar monitoring of Arctic fox: benefits, opportunities, challenges and recommendations. – Polar Res. 36: 2.

Bjørnstad, O. N., Falck, W. and Stenseth, N. C. 1995. A geographic gradient in small rodent density fluctuations: a statistical modelling approach. – Proc. R. Soc. Ser. B 262: 127–133.

Blackburn, T. M. 2004. Method in macroecology. – Basic Appl. Ecol. 5: 401–412.

Blumentrath, S. and Hanssen, F. 2010. Beregning av areal. – In: Nybø (ed), Datagrunnlaget for 'Naturindeks i Norge 2010'. DN-utredning 4-2010, in Norwegian.

Bondrup-Nielsen, S. 1987. Demography of *Clethrionomys gapperi* in different habitats. – Can. J. Zool. 65: 277–283.

Bondrup-Nielsen, S. and Ims, R. A. 1988. Predicting stable and cyclic populations of *Clethrionomys*. – Oikos 52: 178–185.

Boonstra, R. and Krebs, C. J. 2012. Population dynamics of red-backed voles (*Myodes*) in North America. – Oecologia 168: 601–620.

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F.-J. W., Brown, R., Bhatt, U. S., Euskirchen, E. S. and Romanovsky, V. E. 2019. Key indicators of Arctic climate change: 1971–2017. – Environ. Res. Lett. 14: 045010.

Buckley, Y. M. and Puy, J. 2022. The macroecology of plant populations from local to global scales. – New Phytol. 233: 1038–1050.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

CAFF 2013. Arctic biodiversity assesment. Status and trends in Arctic biodiversity. – Conservation of Arctic Flora and Fauna.

Callaway, R., Holt, R. D., Källersjö, M., MacLean, D. A., Magurran, A., Moore, A., Moss, B., Sæther, B.-E., Wedell, N. and Willis, K. 2012. International evaluation of ecology and evolutionary biology in Finland 2006–2010. Evaluation Report. – Publications of the Academy of Finland 3/12.

Cavia, R., Cueto, G. R. and Suárez, O. V. 2009. Changes in rodent communities according to the landscape structure in an urban ecosystem. – Landscape Urban Plan. 90: 11–19.

Cockburn, A. and Lidicker, W. Z. 1983. Microhabitat heterogeneity and population ecology of an herbivorous rodent, *Microtus californicus*. – Oecologia 59: 167–177.

Cornulier, T. et al. 2013. Europe-wide dampening of population cycles in keystone herbivores. – Science 340: 63–66.

Dalkvist, T., Sibly, R. M. and Topping, C. J. 2011. How predation and landscape fragmentation affect vole population dynamics. – PLoS One 6: 0022834.

Delattre, P., De Sousa, B., Fichet-Calvet, E., Quéré, J. P. and Giraudoux, P. 1999. Vole outbreaks in a landscape context: evidence from a six year study of *Microtus arvalis*. – Landscape Ecol. 14: 401–412.

Domine, F., Gauthier, G., Vionnet, V., Fauteux, D., Dumont, M. and Barrere, M. 2018. Snow physical properties may be a significant determinant of lemming population dynamics in the High Arctic. – Arct. Sci. 4: 813–826.

Ecke, F., Angeler, D. G., Magnusson, M., Khalil, H. and Hörnfeldt, B. 2017. Dampening of population cycles in voles affects small mammal community structure, decreases diversity, and increases prevalence of a zoonotic disease. – Ecol. Evol. 7: 5331–5342.

Ecke, F., Benskin, J. P., Berglund, Å. M. M., de Wit, C. A., Engström, E., Plassmann, M. M., Rodushkin, I., Sörlin, D. and Hörnfeldt, B. 2020. Spatio-temporal variation of metals and organic contaminants in bank voles (*Myodes glareolus*). – Sci. Total Environ. 713: 136353.

Ehrich, D. et al. 2020. Documenting lemming population change in the Arctic: can we detect trends? – Ambio 49: 786–800.

Ekerholm, P., Oksanen, L. and Oksanen, T. 2001. Long-term dynamics of voles and lemmings at the timberline and above the willow limit as a test of hypotheses on trophic interactions. – Ecography 24: 555–568.

Erb, J., Stenseth, N. C. and Boyce, M. S. 2000. Geographic variation in population cycles of Canadian muskrats (*Ondatra zibethicus*). – Can. J. Zool. 78: 1009–1016.

Fuglei, E. et al. 2020. Circumpolar status of Arctic ptarmigan: population dynamics and trends. – Ambio 49: 749–761.

Gauthier, G. et al. 2024. Taking the beat of the Arctic: are lemming population cycles changing due to winter climate? – Proc. R. Soc. Ser. B 291: e02361.

Gouveia, A., Bejček, V., Flousek, J., Sedláček, F., Šťastný, K., Zima, J., Yoccoz, N. G., Stenseth, N. C. and Tkadlec, E. 2015. Long-term pattern of population dynamics in the field vole from central Europe: cyclic pattern with amplitude dampening. – Popul. Ecol. 57: 581–589.

Haase, P., Frenzel, M., Klotz, S., Musche, M. and Toll, S. 2016. The long-term ecological research (LTER) network: relevance, current status, future perspective and examples from marine, freshwater and terrestrial long-term observation. – Ecol. Indic. 65: 1–3.

Hansen, B. B., Grotan, V., Aanes, R., Saether, B. E., Stien, A., Fuglei, E., Ims, R. A., Yoccoz, N. G. and Pedersen, A. O. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. – Science 339: 313–315.

Hanski, I., Hansson, L. and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – J. Anim. Ecol. 60: 353–367.

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. and Turchin, P. 2001. Small-rodent dynamics and predation. – Ecology 82: 1505–1520.

Hanssen-Bauer, I., Førland, E. J., Haddeland, I., Hisdal, H., Mayer, S., Nesje, A., NIlsen, J. E. Ø., Sandven, S., Sandø, A. B., Sorteberg, A. and Ådlandsvik, B. 2015. Klima I Norge 2100 – Kunnskapsgrunnlag for klimatilpasning. – In: KSS Rapport, p. 203, in Norwegian.

Hansson, L. 1969. Spring populations of small mammals in central Swedish Lapland in 1964–68. – Oikos 20: 431–450.

Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents - the importance of latitude and snow cover. – Oecologia 67: 394–402.

Hansson, L. and Henttonen, H. 1988. Rodent dynamics as community processes. – Trends Ecol. Evol. 3: 195–200.

Hastings, A., Abbott, K. C., Cuddington, K., Francis, T., Gellner, G., Lai, Y.-C., Morozov, A., Petrovskii, S., Scranton, K. and Zeeman, M. L. 2018. Transient phenomena in ecology. – Science 361: eaat6412.

Henttonen, H., Mcguire, A. D. and Hansson, L. 1985. Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. – Ann. Zool. Fenn. 22: 221–227.

Henden, J.-A., Bårdsen, B.-J., Yoccoz, N. G. and Ims, R. A. 2008. Impacts of differential prey dynamics on the potential recovery of endangered Arctic fox populations. – J. Appl. Ecol. 45: 1086–1093.

Henden, J. A., Ims, R. A. and Yoccoz, N. G. 2009. Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. – J. Anim. Ecol. 78: 636–645.

Henden, J.-A., Ims, R. A., Yoccoz, N. G., Sørensen, R. and Killengreen, S. T. 2011. Population dynamics of tundra voles in relation to configuration of willow thickets in southern Arctic tundra. – Polar Biol. 34: 533–540.

Hijmans, R. J. and Etten, J. V. 2012. raster: geographic analysis and modeling with raster data. R package ver. 2.0-12. – https://CRAN.R-project.org/package=raster.

Hope, A. G., Headlee, K. M., Olson, Z. H. and Wiens, B. J. 2023. Systematics, biogeography and phylogenomics of northern bog lemmings (Cricetidae), cold-temperate rodents of conservation concern under global change. – Syst. Biodivers. 21: 2237050.

Ims, R. A. and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. – BioScience 55: 311–322.

Ims, R. A. and Yoccoz, N. G. 2017. Ecosystem-based monitoring in the age of rapid climate change and new technologies. – Curr. Opin. Environ. Sust. 29: 170–176.

Ims, R. A., Yoccoz, N. G. and Killengreen, S. T. 2011. Determinants of lemming outbreaks. – Proc. Natl Acad. Sci. USA 108: 1970–1974.

Ims, R. A., Henden, J. A., Thingnes, A. V. and Killengreen, S. T. 2013. Indirect food web interactions mediated by predator–rodent dynamics: relative roles of lemmings and voles. – Biol. Lett. 9: 20130802.

Johnson, D. R., Swanson, B. J. and Eger, J. L. 2000. Cyclic dynamics of eastern Canadian ermine populations. – Can. J. Zool. 78: 835–839.

Jolly, S. R., Gilbert, J. H., Woodford, J. E., Eklund, D. and Pauli, J. N. 2024. Seasonal dynamics of small mammal populations: resource availability and cold exposure interact to govern abundance. – Can. J. Zool. 102: 907–921.

Kausrud, K. L., Mysterud, A., Steen, H., Vik, J. O., Ostbye, E., Cazelles, B., Framstad, E., Eikeset, A. M., Mysterud, I., Solhoy, T. and Stenseth, N. C. 2008. Linking climate change to lemming cycles. – Nature 456: 93–97.

Kendall, B. E., Prendergast, J. and Bjørnstad, O. N. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. – Ecol. Lett. 1: 160–164.

Kerr, J. T., Kharouba, H. M. and Currie, D. J. 2007. The macroecological contribution to global change solutions. – Science 316: 1581–1584.

Khalil, H., Ecke, F., Evander, M., Magnusson, M. and Hörnfeldt, B. 2016. Declining ecosystem health and the dilution effect. – Sci. Rep. 6: 31314.

Killengreen, S. T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N. G. and Ims, R. A. 2011. The importance of marine vs human-induced subsidies in the maintenance of an expanding mesocarnivore in the Arctic tundra. – J. Anim. Ecol. 80: 1049–1060.

Kleiven, E. F., Framstad, E., Bakkestuen, V., Böhner, H., Cretois, B., Frassinelli, F., Ims, R. A., Jepsen, J. U., Soininen, E. M. and Eide, N. E. 2022. New national monitoring of small rodents in Norwegian Arctic and alpine tundra based on camera traps. Proposed sampling design and data processing. – In: NINA Report. Norwegian Institute for Nature Research, in Norwegian.

Klemola, T., Tanhuanpää, M., Korpimäki, E. and Ruohomäki, K. 2002. Specialist and generalist natural enemies as an explanation for geographical gradients in population cycles of northern herbivores. – Oikos 99: 83–94.

Korpela, K., Delgado, M., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Yoccoz, N. G. and Huitu, O. 2013. Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. – Global Change Biol. 19: 697–710.

Krebs, C. J. 2013. Population fluctuations in rodents. – The Univ. Press of Chicago.

Krebs, C. J., Boonstra, R., Gilbert, B. S., Kenney, A. J. and Boutin, S. 2019. Impact of climate change on the small mammal community of the Yukon boreal forest. – Integr. Zool. 14: 528–541.

Lidicker, J. and William, Z. 2000. A food web/landscape interaction model for microtine rodent density cycles. – Oikos 91: 435–445.

Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., Dickman, C. R., Hoffmann, A. A., Keith, D. A., Liddell, M. J., Lowe, A. J., Metcalfe, D. J., Phinn, S. R., Russell-Smith, J., Thurgate, N. and Wardle, G. M. 2012. Value of long-term ecological studies. – Austral Ecol. 37: 745–757.

Magnusson, M., Hörnfeldt, B. and Ecke, F. 2015. Evidence for different drivers behind long-term decline and depression of density in cyclic voles. – Popul. Ecol. 57: 569–580.

Mazerolle, M. J. 2012. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c), ver. 1.24. – https://CRAN.R-project.org/package=AICcmodavg.

Moen, A. 1998. Nasjonalatlas for Norge: vegetasjon. – Statens Kartverk, in Norwegian.

Murray, D. L. 2000. A geographic analysis of snowshoe hare population demography. – Can. J. Zool. 78: 1207–1217.

Myers, J. H. 2018. Population cycles: generalities, exceptions and remaining mysteries. – Proc. R. Soc. B 285: 20172841.

Mölle, J. P., Kleiven, E. F., Ims, R. A. and Soininen, E. M. 2021. Using subnivean camera traps to study arctic small mammal community dynamics during winter. – Arct. Sci. 8: 183–199.

Niklasson, B., Hörnfeldt, B., Lundkvist, A., Bjorsten, S. and Leduc, J. 1995. Temporal dynamics of Puumala virus antibody prevalence in voles and of nephropathia epidemica incidence in humans. – Am. J. Trop. Med. 53: 134–140.

Oliver, T. H., Stefanescu, C., Páramo, F., Brereton, T. and Roy, D. B. 2014. Latitudinal gradients in butterfly population variability are influenced by landscape heterogeneity. – Ecography 37: 863–871.

Pall, P., Tallaksen, L. M. and Stordal, F. 2019. A climatology of rain-on-snow events for Norway. – J. Clim. 32: 6995–7016.

Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. – Ecology 86: 2320–2328.

Post, E. et al. 2009. Ecological dynamics across the arctic associated with recent climate change. – Science 325: 1355–1358.

Ravolainen, V. T., Bråthen, K. A., Ims, R. A., Yoccoz, N. G., Henden, J. A. and Killengreen, S. T. 2011. Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. – Basic Appl. Ecol. 12: 643–653.

Ruffino, L., Oksanen, T., Hoset, K. S., Tuomi, M., Oksanen, L., Korpimäki, E., Bugli, A., Hobson, K. A., Johansen, B. and Mäkynen, A. 2016. Predator–rodent–plant interactions along a coast–inland gradient in Fennoscandian tundra. – Ecography 39: 871–883.

Rydgren, K., Økland, R. H., Picó, F. X. and de Kroon, H. 2007. Moss species benefits from breakdown of cyclic rodent dynamics in boreal forests. – Ecology 88: 2320–2329.

Sæther, B. E., Lillegård, M., Grøtan, V., Drever, M. C., Engen, S., Nudds, T. D. and Podruzny, K. M. 2008. Geographical gradients in the population dynamics of North American prairie ducks. – J. Anim. Ecol. 77: 869–882.

Saitoh, T., Stenseth, N. C. and Bjørnstad, O. N. 1998. The population dynamics of the vole *Clethrionomys rufocanus* in Hokkaido, Japan. – Res. Popul. Ecol. 40: 61–76.

Schmidt, J. H., Rexstad, E. A., Roland, C. A., McIntyre, C. L., MacCluskie, M. C. and Flamme, M. J. 2018. Weather-driven change in primary productivity explains variation in the amplitude of two herbivore population cycles in a boreal system. – Oecologia 186: 435–446.

Scott, A. M., Gilbert, J. H. and Pauli, J. N. 2022. Small mammal dynamics in snow-covered forests. – J. Mammal. 103: 680–692.

Sipari, S., Khalil, H., Magnusson, M., Evander, M., Hörnfeldt, B. and Ecke, F. 2022. Climate change accelerates winter transmission of a zoonotic pathogen. – Ambio 51: 508–517.

Soininen, E. M., Ravolainen, V. T., Bråthen, K. A., Yoccoz, N. G., Gielly, L. and Ims, R. A. 2013a. Arctic small rodents have diverse diets and flexible food selection. – PLoS One 8: e68128.

Soininen, E. M., Zinger, L., Gielly, L., Bellemain, E., Bråthen, K. A., Brochmann, C., Epp, L. S., Gussarova, G., Hassel, K., Henden, J.-A., Killengreen, S. T., Rämä, T., Stenøien, H. K., Yoccoz, N. G. and Ims, R. A. 2013b. Shedding new light on the diet of Norwegian lemmings: DNA metabarcoding of stomach content. – Polar Biol. 36: 1069–1076.

Soininen, E. M., Henden, J. A., Ravolainen, V. T., Yoccoz, N. G., Bråthen, K. A., Killengreen, S. T. and Ims, R. A. 2018. Transferability of biotic interactions: temporal consistency of arctic plant–rodent relationships is poor. – Ecol. Evol. 8: 9697–9711.

Soininen, E. M., Magnusson, M., Jepsen, J. U., Eide, N. E., Yoccoz, N. G., Angerbjörn, A., Breisjøberget, J. I., Ecke, F., Ehrich, D., Framstad, E., Henttonen, H., Hörnfeldt, B., Killengreen, S., Olofsson, J., Oksanen, L., Oksanen, T., Tveito, O. E. and Ims, R. A. 2024. Data from: Macroecological patterns of rodent population dynamics shaped by bioclimatic gradients. – Dryad Digital Repository, https://doi.org/10.5061/dryad.h9w0vt4t6.

Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – Oikos 87: 427–461.

Stenseth, N. C. and Framstad, E. 1980. Reproductive effort and optimal reproductive rates in small rodents. – Oikos 34: 23–34.

Stenseth, N. C. and Ims, R. A. 1993. The biology of lemmimgs. – The Linnean Society of London by Acad. Press.

Sæther, B. E., Lillegård, M., Grotan, V., Drever, M. C., Engen, S., Nudds, T. D. and Podruzny, K. M. 2008. Geographical gradients in the population dynamics of North American prairie ducks. – J. Anim. Ecol. 77: 869–882.

Tkadlec, E. and Stenseth, N. C. 2001. A new geographical gradient in vole population dynamics. – Proc. R. Soc. B 268: 1547–1552.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. – Princeton Univ. Press.

Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. and Henttonen, H. 2000. Are lemmings prey or predators? – Nature 405: 562–565.

Tveito, O. E., Bjørdal, I., Skjelvåg, A. O. and Aune, B. 2005. A GIS-based agro-ecological decision system based on gridded climatology. – Meteorol. Appl. 12: 57–68.

Virtanen, R., Oksanen, L., Oksanen, T., Cohen, J., Forbes, B. C., Johansen, B., Käyhkö, J., Olofsson, J., Pulliainen, J. and Tømmervik, H. 2016. Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome. – Ecol. Evol. 6: 143–158.

Wiens, J. A. 1989. Spatial scaling in ecology. – Funct. Ecol. 3: 385–397.

Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N. and Spence, K. O. 2010. A meta-analysis of resource pulse–consumer interactions. – Ecol. Monogr. 80: 125–151.