Macroecological patterns of rodent population dynamics shaped by bioclimatic gradients

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Abstract

Long-term studies of cyclic rodent populations have contributed fundamentally to the development of population ecology. Previous research has shown macroecological patterns of population dynamics in relation to latitude, but without disentangling the role of underlying ecological and climate drivers. We collected 26 rodent time-series from the tundra biome and assessed how population dynamics characteristics of the most prevalent species varied with latitude and environmental variables. While we could not find a relationship between latitude and population cycle peak interval, other characteristics of population dynamics had latitudinal patterns. The environmental predictor variables provided insight into causes of these patterns, as i) increased proportion of optimal habitat in the landscape led to higher population cycle amplitudes in all species and ii) mid-winter climate variability had negative impacts on cycle 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.

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most prevalent species varied with latitude and environmental variables. While we could not find a relationship between latitude and population cycle peak interval, other characteristics of population dynamics had latitudinal patterns. The environmental predictor variables provided insight into causes of these patterns, as i) increased proportion of optimal habitat in the landscape led to higher population cycle amplitudes in all species and ii) mid-winter climate variability had negative impacts on cycle 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

Introduction

Studies of the cyclic population dynamics of small rodents have contributed greatly to our understanding of population dynamics (Berryman 2002, Stenseth 1999, Turchin 2003). In particular, long-term series have provided an opportunity for macroecological studies (Cornulier et al. 2013, Ehrich et al. 2020, Hansson and Henttonen 1985). Such studies can reveal general patterns across large scales, enabling comparisons of climatic and ecological drivers of population dynamics and ecosystem functioning (Blackburn 2004, Kerr et al. 2007). Notably, many of the previous large-scale analyses of Fennoscandian rodents have shown strong latitudinal clines, with a northward increase in rodent cycle peak interval and amplitude (Bjørnstad et al. 1995, Hanski et al. 2001, Hansson and Henttonen 1988, Korpela et al. 2013, but see Angerbjörn et al. 2001). This gradient and its suggested connection to a species richness gradient within the predator guild has found its way into major ecology text books (Begon et al. 2006). Some studies based on exceptionally long-term data have, however, indicated that such macroecological pattern may be transient (Henden et al. 2009, Steen et al. 1990).

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. Examples of such hypotheses are the roles of food-web interactions (Hanski et al. 2001, Oksanen et al. 2008), diseases (Burthe et al. 2006), species-specific traits (Andreassen et al. 2013), landscape configuration (Magnusson et al. 2015), and climate (Kausrud et al. 2008, Tkadlec and Stenseth 2001) in shaping rodent dynamics. Although surrogate variables such as latitude and altitude may provide valuable clues about the underlying processes, quantification of more mechanistic variables is needed to reach beyond pattern description (Krebs 2013). Typically, several environmental variables change along latitudinal and altitudinal gradients, making their respective effects difficult to disentangle. For instance, previous studies of the Fennoscandian latitudinal gradient have merged data from different biomes (e.g. boreal forest and tundra) and the different rodent communities specific to these biomes (Bjørnstad et al. 1995, Hanski et al. 1991).

We propose that focusing on macroecological patterns of rodent population dynamics within a single biome allows for stronger inferences owing to less confounding between ecological and climatic variables. We first assessed whether biome-specific analyses of Fennoscandian rodents detected similar latitudinal patterns of population cycle characteristics as previous studies. We focused on the tundra biome, as rodent cycles 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 hypothesized that the Norwegian lemming (*Lemmus lemmus*), the only rodent species endemic to the Fennoscandian tundra, is more sensitive to more variable winter climate than other tundra-dwelling rodent species (Ims et al. 2011, Kausrud et al. 2008). Accordingly, we predicted that in regions with more variable winter climate the lemming makes up a smaller proportion of the rodent community and has lower amplitude cycles. We further hypothesized that landscape structure has implications for both rodent community structure and species-specific cycle amplitudes, as maximum population growth rates and consequently highest amplitudes should be related to high proportions of optimal habitat in the landscape (Bondrup-Nielsen and Ims 1988, Dalkvist et al. 2011, Lidicker 2000). Accordingly, we predicted that different rodent species would both dominate the rodent community and reach the highest cycle 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, see Table A3). 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; besides 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 captured species were available for [?] 10 years (Table 1, Figures 1 and A1, Appendix 2). Some of the locations also included trapping in adjacent ecotone forests (Appendix 2). The time-series at the different locations have 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 km^2 to >1000 km^2(Appendix 2).

For analyses at the sampling unit level, we excluded sampling units if i) trapping had been conducted less than 10 years, unless a new unit was established in the vicinity to replace the previous unit, ii) the time-series were disconnected by gap years resulting in shorter than 10 years of continuous data or iii) no rodents were ever trapped. We also excluded locations from these analyses if data were not available per sampling unit. In total, 22 locations (n = 385 sampling units) fulfilled all criteria.

We used data from 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 i) included sampling season as an additive factor in all regression models, and ii) 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.

Characteristics of rodent population dynamics

We focused on characteristics of rodent population dynamics that have consequences for ecosystem functioning, namely *cycle amplitude* ,*peak interval, peak sharpness* , *mean densities* and*community contribution* (cf. Hanski et al. 1991, Henden et al. 2008, Krebs 2013, Turchin et al. 2000, Table A1). Variables and their calculation are described in Table 2.

We assessed the presence of temporal trends in community contribution (Text A4, Figure A12, Table A12). As no such trends were evident, we proceeded with the approach of using rodent population cycle characteristics aggregated over time as spatial replicates.

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 km^2, 9 km^2, and 25 km^2 around each sampling unit. Because the results differed only little, we present only 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 km^2, 9 km^2 and 25 km^2, respectively). Results at other extents are given in Text A2, Tables A8, A9, Figures A6, A7.

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 would represent a more variable winter climate as the baseline is 0 or very low number of days with temperature above 0°C (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 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 x 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 km x 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 (Table A3, Moen 1998), published by Blumentrath and Hanssen (2010). The map is based on modeling the tree-line altitude and thereafter estimating the elevation limits of the bioclimatic zones (Blumentrath and Hanssen 2010). The map has pixel size 25m x 25m. 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 km x 5 km) square and calculating the proportions of bioclimatic zones within the square. Second, we used July mean temperature (degC) 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 degC +- sd): low alpine (10.6 +- 1.3), middle alpine (8.7 +- 1.5), and high alpine zone (6.8 +- 1.4) (Figure A4). 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 rodent genus and each characteristic, 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 (Bjornstad et al. 1995, Hansson and Henttonen 1985), 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 population dynamics characteristics, focusing on community contribution and amplitude. We constructed two model sets: i) *model set for all data* (n=385 sampling units from 22 locations) using July temperature and winter climate variability as predictor variables, and ii)*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, Figure 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 population dynamics characteristics beyond the extent of location. To do this, we assessed the evidence for a spatial autocorrelation of the predicted random effects for location (Text A3, Figures A10, A11, Table A10). When there was evidence for such autocorrelation, it could be removed by including latitude as an additional covariate (Table A10), and we checked if results were robust to the inclusion of latitude as a covariate (Table A11). We selected the best models in each candidate model set based on $\mathrm{AICc_c}$ (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, 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

Characteristics of rodent population dynamics

At the sampling unit level, the community contributions of all three rodents ranged from 0-100% (Table A2). 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 (Figure 1b, Table A2).

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 to 6.8 (mean 3.8 years, Table A2). 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, Table A2).

At the sampling unit level, mean density was the population dynamics characteristic with clearest differences between the rodent genera (Figure 2, see Table A2 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 slightly lower than those of voles (2.3, 2.8, and 2.5 for lemmings, grey-sided voles, and *Microtus* , respectively). 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 characteristics of population dynamics were connected in all species in a similar manner (Figure A3). 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 (Figure A3). 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 (Figures 2, A3), indicating that sharp peaks were a consistent characteristic of this species.

Latitudinal patterns of population dynamics

The relationship to latitude differed between species (Figure 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 (Figure 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 (Table A5, Figure A5). Location level peak interval had no clear latitudinal trends, either. We explored visually patterns between peak interval and other variables (location, environmental variables, Figures A2, A9), 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 degC (for all values in this paragraph, see Table A4). 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 (Figure A8).

For lemmings, high community contribution and high amplitudes were related to the colder parts of the landscape (see Table 4 and Figure 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, with an increasing impact at higher temperatures. 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 (Tables A6, A7).

Discussion

Our study is the first biome-specific macroecological analysis of a rodent community at the scale of a biogeographic region (i.e., Fennoscandia). Earlier studies based on rodent trapping series from Fennoscandia have been instrumental for demonstrating macroecological latitudinal patterns of vertebrate community dynamics (Angelstam et al. 1984, 1985, Bjornstad et al. 1995, Hanski et al. 1991, Hansson and Henttonen 1985, Steen et al. 1990) and as baselines for generating hypotheses of the underlying drivers of these dynamics (e.g. Hanski et al. 1993, Hanski et al. 2001, Hansson and Henttonen 1988, Korpela et al. 2013, Korpela et al. 2014). Our approach enabled us to verify that the previously found latitudinal gradient of the cycle amplitude was also present within the tundra biome, albeit only found in voles and not in lemmings. In contrast, we found no evidence for the previously found northwards increasing peak interval (Bjornstad et al. 1995, Hanski et al. 2001). Further, the rodent community characteristics were related to landscape composition. Thus, bioclimatic zonation appears to be a strong predictor of structure and functioning of tundra rodent communities and as such more informative than latitudinal gradients. Furthermore, increasing winter climate variability decreased cycle 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. Some of the relationships we identified were species-specific, demonstrating that lumping functionally different species in analyses of population dynamics characteristics should be done with great care, as it may mask relevant species-specific patterns. Even the lumping of two ecologically similar *Microtus* species in the present analyses may have affected our results. Taken together, environmental variables provided new understanding beyond latitudinal patterns.

Voles and lemmings have been described to have distinct shapes of the cycles, with vole peaks being of lower amplitude and rounder than those of lemmings (Turchin et al. 2000). Although we found lemming peaks to be on average sharper than vole peaks, their cycle amplitudes were within the same range as those of voles. Our results of cycle topology are thus only partly in line with the hypothesis by Turchin et al. (2000), i.e. different trophic interactions creating the different shapes of rodent population cycles. Moreover, our results on cycle topologies may relate to lemming peaks being observed less frequently than vole peaks, often with no individuals during the low phase, which can result from the scarcity of time-series sampling lemmings in their optimal bioclimatic zone (middle alpine), or different trappability. The community contribution of lemmings increased together with the proportion of middle alpine bioclimatic zone of the landscape, conforming well to smaller scale studies (Ekerholm et al. 2001, Ims et al. 2011, Kleiven et al. 2018). We thus expect that time-series collected in the middle alpine bioclimatic zone could have higher lemming cycle amplitudes than those observed in the existing data. Comparing lemming data from the middle alpine zone against vole data from the low alpine zone would relate each species to their optimal parts of the landscape, and thus provide a better case for comparing cycle topologies.

Our results matched only partly the earlier macroecological descriptions of Fennoscandian rodent population dynamics (Angerbjorn et al. 2001, Bjornstad et al. 1995, Hanski et al. 1991, Hansson and Henttonen 1988, Korpela et al. 2013). In particular, we found no support for the latitudinal gradient in rodent population peak interval, unlike Bjornstad et al. (1995), and Hanski et al. (1991). A lack of patterns within the tundra biome could indicate that this pattern arises from comparisons between biomes (e.g. less variable peak intervals in the tundra than in the boreal biome). Furthermore, it is unlikely that peak interval remains fixed over several decades, given the variation observed across Norway during the 20th century (Henden et al. 2009, Steen et al. 1990). Our findings thus support the conclusion of Henden et al. (2009); that the latitudinal gradient of small rodent population dynamics characteristics in Fennoscandia is not a temporally persistent phenomena and may rather be a case of transient dynamics (Hastings et al. 2018).

The species-specific properties of population dynamics did, however, show some of the same latitudinal patterns as described earlier (e.g. Hanski et al. 1991, Hansson and Henttonen 1985). The cycle amplitude of both vole species increased northwards, and the grey-sided vole displayed a prominent northward increase of community contribution, mean density, and cycle amplitude, concurrently with increasingly round peaks. However, both the abundance of low alpine bioclimatic zone (for Norway) and July temperature (for all locations) were positively correlated with latitude. Thus, the latitudinal patterns of voles appear to be related to an increasing abundance of the optimal bioclimatic zone in the landscape (cf. Bondrup-Nielsen and Ims 1988, Lidicker 2000). An increasing quality of the low alpine zone vegetation towards north, in terms of increasing palatability (Virtanen et al. 2016), could also contribute to explain this pattern.

Population dynamics of lemmings showed little latitudinal patterns, except for a decreasing community contribution towards the north. On the other hand, landscape composition appears to be a stronger predictor of the species dynamics than latitude, as both cycle amplitude and community contribution of lemmings had a positive relationship with the colder parts of the landscape. Our findings thus support the idea that landscape structure is an important determinant of both rodent community structure (Ecke et al. 2017) and species-specific population dynamics (Bondrup-Nielsen and Ims 1988, Le Vaillant et al. 2018, Lidicker 2000, Magnusson et al. 2015, Pyke et al. 1977).

We found little evidence for winter climate impacts on lemming community contribution. Yet, variable winter climate and community composition appear related, as the frequency of above-zero winter temperatures was positively associated with the community contribution of grey-sided voles. Furthermore, population cycle amplitude of lemmings and grey-sided voles decreased with increasing winter climate variability. Andreassen et al. (2020) found a similar pattern in boreal forests, relating the highest vole cycle amplitudes to the highest altitudes with presumably the coldest winters. Similarly, Ruffino et al. (2016) found a higher lemming peak in a continental study area with presumably colder winter climate than in a coastal study area, but an opposite pattern for grey-sided voles. Our results are thus only partly in line with these more local studies, but it appears evident that winter climate variability can affect both rodent community composition and the cycle amplitudes of both voles and lemmings.

Lemmings have been suggested to be more sensitive to warm winter climate than voles, potentially because their low-growing food plants can easily be encapsulate by ice after melt-freeze events (Ims et al. 2008, Ims et al. 2011). Our analyses did not reveal any dichotomy between lemmings and grey-sided voles in terms of winter climate effects but provided less evidence for the *Microtus* -voles sensitivity for winter climate than for the other tundra rodents. These seemingly contrasting results among the genera must, however, be interpreted with caution. First, lemmings and *Microtus* voles were scarce in most locations (n=5 and n=2 locations with more than 50% lemmings and *Microtus* , respectively), which potentially affected our ability to detect strong winter climate impacts in these genera. Moreover, although within-year spring and fall abundances are usually well correlated (Cornulier et al. 2013, Kausrud et al. 2008), winter climate is expected to have the most direct impact on spring abundances. Indeed, previous local-scale studies demonstrating impact of winter climate in *Microtus* and lemmings were based on population growth rates between fall and spring (Aars and Ims 2002). Thus, winter climate impacts are more likely to be revealed by analyses of e.g., snap-trapping data from the spring or by camera trapping data collected throughout the year. Furthermore, our variable for winter climate was calculated from gridded meteorological data across fixed mid-winter dates. Locally measured data on snow structure would provide a more mechanistic variable (Domine et al. 2018, Kausrud et al. 2008), while winter length can be decisive for cyclicity (Bierman et al. 2006). 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.

Future perspectives

We propose that the Fennoscandian tundra and its rodent community are well suited for further biome-specific macroecological studies. The tundra biome extends across more than 10 latitudinal degrees in Fennoscandia and covers distinct climate gradients (Moen 1998, Virtanen et al. 2016), and small rodent dynamics in the tundra appear to have more pervasive food web impacts than in other biomes (Ims and Fuglei 2005, Krebs 2011, Olofsson et al. 2012). We here show that in this region, rodent population dynamics characteristics vary greatly within the biome and between the rodent genera. More focused assessments of causes of such variation have been called for (see 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).

We see considerable scope for improvements for future macroecological studies based on small rodent population time series from the Fennoscandian tundra. Better insight may be achieved by i) extension of small rodent monitoring to achieve greater representation of higher alpine zones, ii) harmonization of practices and protocols, iii) development of environmental predictor data layers across country borders, iv) collection of data on tundra rodent dynamics throughout different seasons (e.g. Molle et al. 2021), and v) development of predictor variables targeting winter climate impacts on rodents.

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, Ecke et al. 2020, Ims and Yoccoz 2017). The scientific community has recognized its importance (Haase et al. 2016, Lindenmayer et al. 2012), but continued funding remains a challenge (Callaway et al. 2012). Yet, continued funding and increased coordination are prerequisites to achieve an efficient macroecological study design. The tundra biome is also the terrestrial biome on earth most affected by climate change (Box et al. 2019, CAFF 2013, Post et al. 2009) and the existing spatial configuration of population cycle characteristics is likely to change accordingly. Monitoring of the tundra biomes' key players according to a macroecological protocol is a valuable approach to detect the impacts of climate change on tundra ecosystem functioning.

Supplementary material

Appendix 1: additional figures, tables, and methodological details

Appendix 2: additional information on rodent-time-series

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Figures

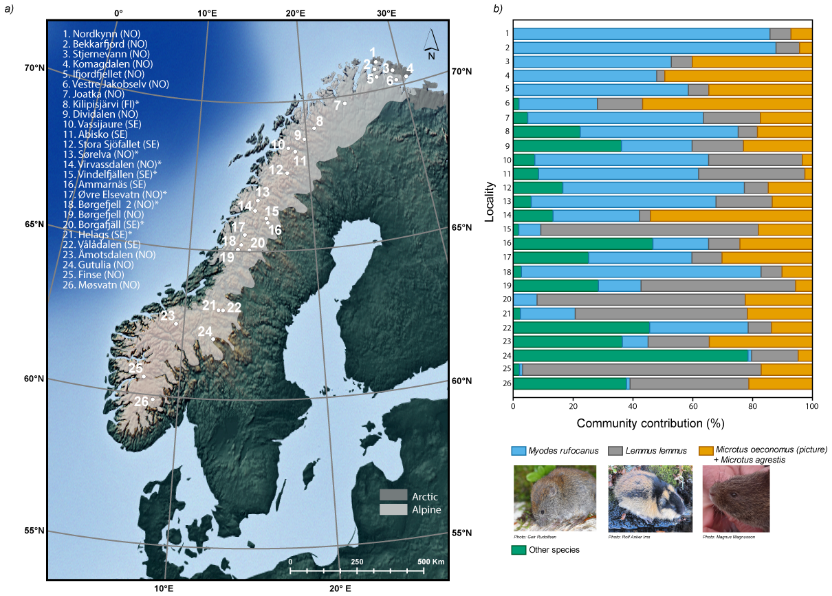

Figure 1. (a) Study areas (n = 26 locations) located in the alpine and arctic regions of Fennoscandia in northern Europe where small rodents have been snap-trapped in fall [?] 10 consecutive years. Locations denoted with * are exceptions (trapping conducted only in spring or/and summer or with gaps in the respective time-series; see details in Table 1). (b) Community contribution of rodent genera within each location: the grey-sided vole (*Myodes rufocanus;* blue bars); Norwegian lemming (*Lemmus lemmus* ; grey bars); field vole (*Microtus agrestis*) and tundra vole (*Microtus oeconomu* s) (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*).

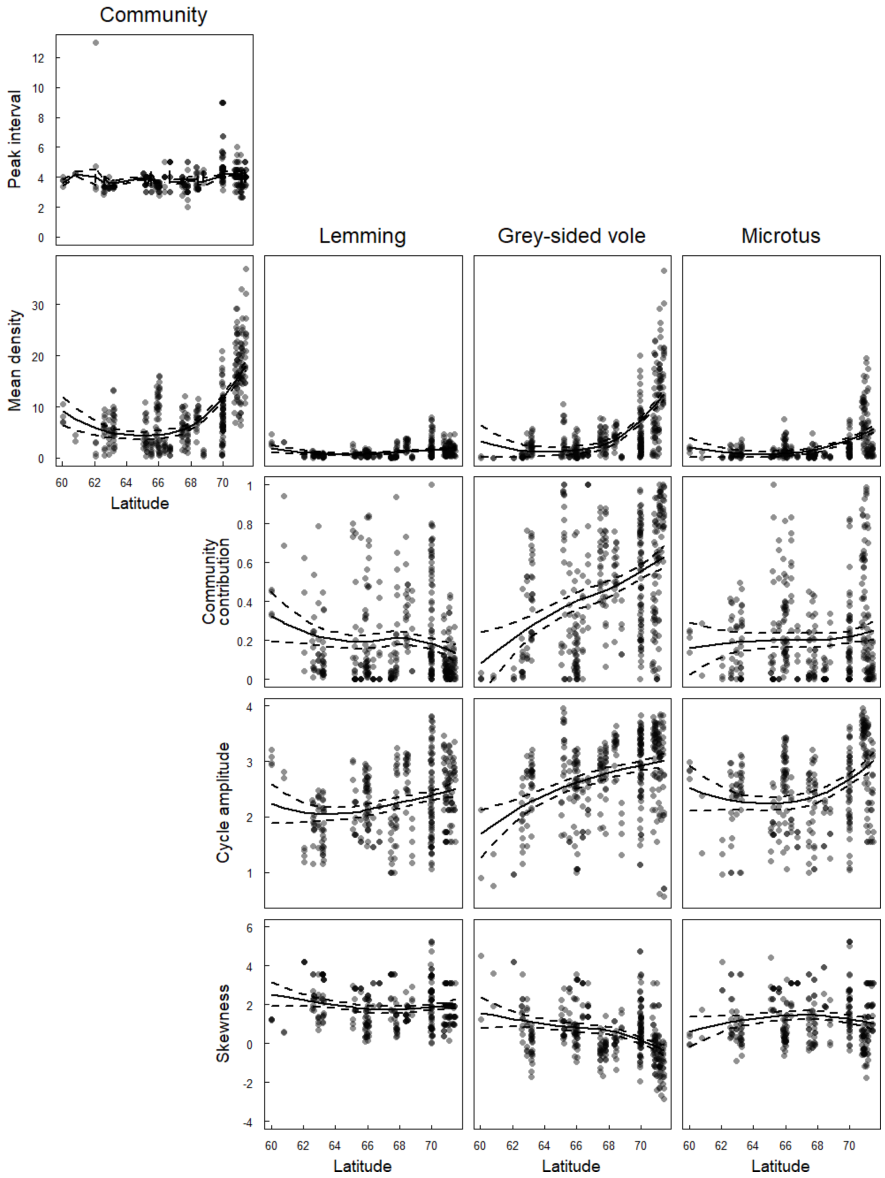

Figure 2. Relationships between latitude and characteristics of small rodent population dynamics in the small rodent community of Fennoscandian tundra, based on 385 sampling units from 22 locations (Table 1a). The plots for peak interval and community contribution include all sampling units. The plots for mean density, cycle 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 and its 95% confidence intervals.

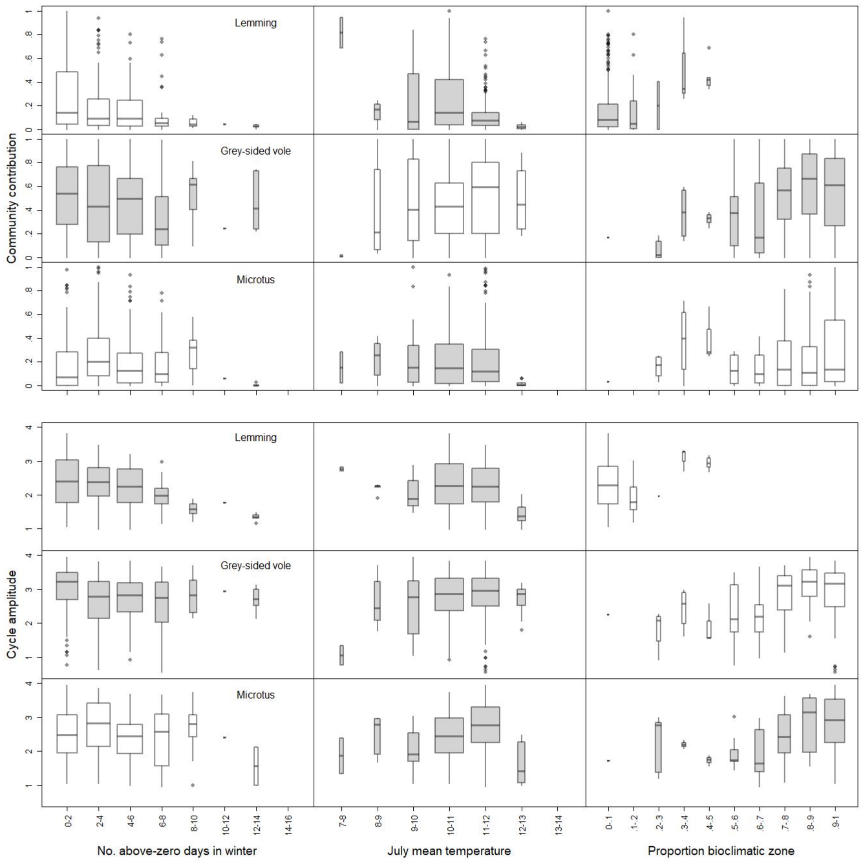

Figure 3. Relationship between environmental predictor variables and characteristics of small rodent population dynamics of Fennoscandian tundra, based on 385 sampling units from 22 locations (Table 1a). The panels for no. of above-zero days in winter and July mean temperature include data form all locations, 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 cycle 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. Environmental variables were calculated across a 25 km^2 buffer zone, for figures with 9 km^2 and 1 km^2 buffers see Appendix 1 (Figures A6 and A7). Grey boxes indicate variables that were statistically significant in the best models in either model set (Table 4).

Tables

Table 1. Description of small rodent snap-trapping time-series included in this study. Time-series in part (a) are included in all analyses and time-series in part (b) only in location level analyses (see Appendix 2 for details). For additional information on the complete time-series see Appendix 2. For all time-series in (a) we only included units that were active [?] 10 years. Time series numbers refers to Figure 1.

(a)

Location	**Period**	**Sampling unit type**	**No. of sampling units/year**	**Trap nights /sampling unit**	**Trapping season (analysed season in bold)**	**Total number of rodents (in the analysed data)**	**Number 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	74	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	20	12-24	**Variable**	343	5.83

Location	**Period**	**Sampling unit type**	**No. of sampling units/year**	**Trap nights /sampling unit**	**Trapping season (analysed season in bold)**	**Total number of rodents (in the analysed data)**	**Number of rodents per 100 trap nights (in the analysed data)**
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 to 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 / yea**
8. Kilpisjärvi (FI)*	1946-2012 (excl. 1948, 1976, 1984, 2010)	Trap line	1-4
15.Vindelfjällen (SE)*	2001-2018 (excl. 2005, 2009,2010, 2011, 2016)	Trap line	2-12
20.Borgafjäll (SE)*	2004-2016 (excl. 2009, 2010, 2014)	Trap line	3-20
21. Helags (SE)*	2001-2018(excl.2003, 2004, 2009, 2016)	Trap line	2-42

* = 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.

Table 2. Description of rodent population dynamics characteristics. Indices for characteristics 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 is conducted (see Table 1). Characteristics denoted with * were also calculated at location level.

Characteristic	Description
Community contribution*	Proportion of a given genus in the community, based on the total number of rodent individuals
Mean density	Mean trapping index, calculated for each rodent genus.
Cycle amplitude	Variability of the population abundance around the mean. Calculated using the standard devia
Peak sharpness	Based on skewness of the data, which is defined as $\gamma_1 = \mu_3/\mu_2^{3/2}$ (μ_2 and μ_3 are the second and
Peak interval*	Mean number of years between population peaks. Calculated based on visual inspection of data

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	Response variable	Model estimates	Model estimates	Model estimate
		Intercept	Fixed effects Latitude	Fixed effects Sampling seaso
Community	Mean density (n=385)	-74.72 (-111.30, -38.26)	**1.13 (0.64, 1.62)***	**-6.64 (-12.12,**
	Peak interval (n=373)	1.20 (-1.79, 4.20)	0.04 (-0.01, 0.07)	-0.26 (-0.26 0.61
Lemming	Community contribution (n=385)	5.36 (-0.92, 11.67)	**-0.10 (-0.18, -0.02)***	**-1.32 (-2.24, -**
	Mean density (n=334)	0.41 (-6.64, 7.51)	0.01 (-0.08, 0.11)	-1.06 (-2.20, 0.0
	Cycle amplitude (n=334)	0.65 (-2.80, 4.11)	0.02 (-0.02, 0.07)	**-0.58 (-1.13, -**
	Skewness (n=334)	3.58 (-1.66, 8.82)	-0.02 (-0.09, 0.05)	0.80 (-0.05, 1.65
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
	Mean density (n=367)	-71.35 (-101.81, -40.89)	**1.03 (0.62, 1.43)***	-3.18 (-7.61, 1.2
	Cycle amplitude (n=367)	-6.39 (-10.22, -2.57)	**0.12 (0.07, 0.17)***	-0.28 (-0.81, 0.2
	Skewness (n=367)	18.79 (12.16, 25.45)	**-0.24 (-0.33, -0.16)***	**1.07 (0.14, 2.0**
Microtus	Community contribution (n=385)	-3.11 (-11.99, 5.76)	0.01 (-0.11, 0.13)	0.38 (-0.94, 1.69
	Mean density (n=305)	-26.17 (-45.68, -6.59)	**0.39 (0.12, 0.65)***	-1.40 (-4.34, 1.5
	Cycle amplitude (n=305)	-3.07 (-7.71, 1.56)	**0.07 (0.01, 0.14)***	-0.48 (-1.18, 0.2
	Skewness (n=305)	3.78 (-4.20, 11.78)	-0.03 (-0.14, 0.07)	**1.38 (0.18, 2.5**

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 cycle 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 Appendix 1 for model selection table (Tables A6, A7) and results at 9 km^2 and 1 km^2 (Tables A8, A9).

Response variable (dataset, sample size)	Response variable (dataset, sample size)	Intercept	Fixed effects
			Winter climate v
Lemming	Community cont. (A, n=385)	5.96 (3.64, 8.12)	**-**

Response variable (dataset, sample size)	Response variable (dataset, sample size)	Intercept	Fixed effects
	Community cont. (N, n=239)	-2.47 (-2.92, -2.01)	**-**
	Cycle amplitude (A, n=334)	5.90 (4.73, 6.99)	-
	Cycle amplitude (N, n=194)	2.80 (2.41, 3.19)	**-0.13 (-0.21, -0**
Grey-sided vole	Community cont. (A, n=385)	-2.03 (-2.65, -1.43)	**0.12 (0.05, 0.1**
	Community cont. (N, n=239)	-0.35 (-1.70,0.92)	-
	Cycle amplitude (A, n=367)	0.88 (-0.38, 2.13)	**-**
	Cycle amplitude (N, n=225)	2.97 (2.47, 3.47)	**-0.12 (-0.22, -0**
Microtus	Community cont. (A, n=385)	-2.13 (-2.67, -1.59)	**-**
	Community cont. (N, n=239)	-2.93 (-4.20, -1.64)	**-**
	Cycle amplitude (A, n=305)	2.53 (2.24, 2.82)	**-**
	Cycle amplitude (N, n=181)	1.66 (1.02, 2.29)	**-**