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Small rodent communities in the changing Arctic

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Cover Image: A Siberian lemming appears from under the snow to feed on the green branches of moss in Yamal Peninsula of Siberia, Russia (see Sokolova et al., e17161). Photo by Natalia Sokolova.

RESEARCH ARTICLE

Expansion of voles and retraction of lemmings over 60 years along a latitudinal gradient on Yamal Peninsula

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Abstract

Range shifts and changes in dominance of species in communities are among the major predicted impacts of climate change on ecosystems, supported by numerous modeling studies. While climate is changing particularly rapidly in the Arctic, little observational data is available to document predicted changes in the composition of communities, in particular from the large Russian tundra areas. Small rodents are a key component of tundra ecosystems implementing important ecological functions both as herbivores and as main prey for a whole guild of predators. Here we document changes over 60 years in occurrence of nine species of small rodents along a latitudinal gradient spanning from the forest-tundra ecotone to the high Arctic tundra on Yamal Peninsula. All data were obtained using a single method: snap-trapping. In general, the occurrence of lemmings, specialized arctic endemics, decreased in the southern parts of the peninsula, whereas the occurrence of voles, representing boreal or wide-spread species, increased and expanded northwards. The occurrence of Siberian lemmings (*Lemmus sibiricus*) in particular declined over the whole latitudinal gradient and possibly disappeared from the southernmost zones, whereas collared lemmings (*Dicrostonyx torquatus*) declined significantly only in the forest tundra. The strongest increase was observed in the tundra zones for narrow-headed voles (*Lasiopodomys gregalis*), a wide-spread species inhabiting meadows and riparian habitats, and Middendorff's voles (*Alexandromys middendorffii*), a primarily low Arctic species inhabiting waterlogged tundra. Both species also expanded their distribution range northwards during the last two decades. The observed changes might be due to the effect of several drivers of environmental change occurring in concert: climate warming both in winter and in summer, and increased human activity notably related to intensive reindeer herding and industrial development.

KEYWORDS

collared lemming, Middendorff's vole, narrow-headed vole, northern red-backed vole, range shift, Siberian lemming, small rodents community, Yamal

1 | INTRODUCTION

Terrestrial arctic ecosystems are experiencing important changes during recent decades (Ims et al., 2013; Ims & Fuglei, 2005). Climate change, that is three to four times more rapid at high latitudes than further south (Chylek et al., 2022), is the main driver of changes in biodiversity, but other anthropogenic impacts, such as industrial development and land-use intensification play a significant role in interacting with climate (IPCC, 2023; Post et al., 2009). Range shifts leading to changes in biodiversity and species assemblages are one of the main predicted consequences of climate change with major impacts on ecosystem functioning, and numerous studies have used modeling to predict such shifts for the future. However, the availability of long-term data to actually document distribution changes at the community level is heavily biased in its geographical and taxonomic distribution, with relatively low representation of the Arctic, where changes are expected to be particularly important, and nearly no data from northern Asia (Lenoir et al., 2020). A recent systematic review included for instance only four data points above 60 latitude and noted that much less studies addressed terrestrial mammals than birds (Ramalho et al., 2023). Existing studies, however, document that important changes indeed do occur for some species (e.g., Gallant et al., 2019; Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016). This scarcity of knowledge is due to the lack of well documented historical data or long-term monitoring programs from remote Arctic locations. A similar lack of data, with notably important gaps in the Russian Arctic, and often short data series, has also been highlighted in circumpolar trend assessments such as the Arctic species trend index (Barry & Helgason, 2019). Existing long-term data on arctic communities are thus very valuable (van Beest et al., 2021).

Climate change impacts Arctic species through numerous pathways, both directly and indirectly (Barry & Helgason, 2019; Ims et al., 2013). Thus, longer growing seasons and higher average summer temperatures lead to changes in plant communities, notably increasing growth of erect shrubs and declines of less competitive groups such as lichen and mosses (Berner et al., 2020; Mekonnen et al., 2021). Climate warming, shrub expansion and changing riparian ecosystems, in turn, drive range expansions of moose and snowshoe hares (*Alces alces* and *Lepus americanus*; Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016). But a shorter and more shallow snow cover increases predation risk for snowshoe hares, making them more conspicuous because of camouflage mismatch (Zimova et al., 2016) and easier to hunt for coyotes, potentially affecting their well-known population cycles (Peers et al., 2020). While climate change is the major driver of change for Arctic communities, it interacts in some regions with anthropogenic interference. In Alaska, for example, industrial development together with summer warming and permafrost thaw led to important geo-ecological changes over the last 60 years (Raynolds et al., 2014). In Scandinavia, high densities of semi-domestic reindeer (*Rangifer tarandus*) can limit the growth of willow shrubs and thus counteract climate driven vegetation changes (Bråthen et al., 2017).

Small rodents, lemmings and voles, are a key component of tundra ecosystems. Lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) in particular, with their conspicuous population cycles, exert a number of important ecological functions: they are an essential prey for a whole guild of more or less specialized predators (e.g., Gilg et al., 2003; Legagneux et al., 2012) and can have major impacts on the vegetation at peak abundance (Olofsson et al., 2012). Moreover, it has been shown that lemming grazing affects CO₂ uptake by Arctic vegetation (Plein et al., 2022), and that the structures created by lemmings in the tundra, such as winter nests, runways and latrines, may impact biogeochemical cycling rates and plant nutrient availability (Roy et al., 2022). Recently, most of the existing long-term data on lemming population dynamics was summarized across the circumpolar Arctic (Ehrich et al., 2020). No general trends were detected, but a decrease was observed for some low arctic lemming populations that were sympatric with voles, highlighting the importance of a community perspective. This study also showed a general scarcity of long-term data about small rodents from the Arctic (except for Fennoscandia), and especially from its Russian sector, representing approximately half of the terrestrial mainland Arctic (Ehrich et al., 2020).

Here we present a unique long-term dataset about small rodent communities over more than 60 years on Yamal Peninsula in the Russian Arctic. The peninsula spans over several bioclimatic subzones and its ecosystems are at present affected by multiple drivers of change: in addition to climate change (e.g., Forbes et al., 2016), rapid industrial development has considerable local impacts (Bogdanov et al., 1997). Yamal also hosts the world's largest population of domestic reindeer, herded in a traditional way by nomadic Nenets people, and their numbers have more than doubled during the last 60 years, reaching now 225,000 animals (FAO, 2022). Moreover, Arctic species (both herbivores and predators) are increasingly exposed to competition with expanding boreal generalists. Regarding small rodents, previous investigations documented a decrease in the amplitude of cyclic fluctuations in the low Arctic tundra that caused a decline in the nesting density of rough-legged buzzards (*Buteo lagopus*; Fufachev et al., 2019).

It is likely that the cumulative effects of climate change, intensive reindeer herding and growing industrial development on ecosystems in Yamal also changed the conditions for small rodents, resulting in changes in the occurrence of different species. In other areas of the Arctic, changes in winter climate, notably changes of snow physical properties and shorter winters, have been shown to be detrimental for lemmings which usually breed under the snow (Duchesne et al., 2011; Gilg et al., 2009; Poirier et al., 2019). In Yamal, several major ground icing events were documented during the last decades, suggesting an increase in unfavorable winter conditions that may have been detrimental to lemmings (Bartsch et al., 2010, 2022; Sokolov et al., 2016). In summer, warmer climate leads to increasing total aboveground biomass (Berner et al., 2020), notably increased growth of willow thickets (Forbes et al., 2010; Mekonnen et al., 2021) and expansion of boreal plant species into the low Arctic. These vegetation changes are likely to increase

the habitat available to more southern small rodent species, notably folivorous voles. Moreover, human activities such as intensive reindeer herding as well as infrastructure development and off-road driving, transform the landscape and can cause vegetation shifts towards non-typical tundra communities dominated by graminoids (Kryazhimskiy et al., 2011; Sokolova & Ektova, 2020; Tuomi et al., 2021). The spread of such habitats could favor the expansion of species living in meadows such as narrow-headed voles (*Lasiopodomys gregalis*; Sokolova, 2004). Overall, given the impact of these different drivers of change on the ecosystem of Yamal and the biology of the different small rodent species, we predict a decrease in occurrence of lemmings, particularly in the southern part of the peninsula over the last decades. At the same time, we predict an increase in the occurrence of vole species, in particular species related to grasslands and willow thickets, and a northward expansion of boreal and low Arctic species.

2 | METHODS

2.1 | Study area and species

Yamal Peninsula is situated in the north of Western Siberia and is surrounded by Baydaratskaya Bay on its western shore and by Obskaya Bay on its eastern shore. To the north, the peninsula is separated from Bely Island by the narrow Malygina Strait. Yamal extends over more than 770 km from south to north and has a relatively constant width of 200–250 km. The relief is homogenous and relatively flat, with a maximum elevation of 92 m above sea level. The landscape includes numerous lakes and rivers but has no significant geographical barriers to dispersal of terrestrial species.

According to long-term climatic data for the western sector of the Russian Arctic, the mean annual air temperature increased on average by 1.4°C for the period 1991–2020 compared to 1960–1990, and the number of days with positive mean temperatures increased on average by 10–14 days (Malkova et al., 2022). Two meteorological stations from Yamal were used for these calculations: Salekhard (forest-tundra, mean annual temperature increased from –5.9 to –4.4°C) and Marre-Sale (subzone D, mean annual temperature increased from –8.5 to –6.9°C). The sum of positive monthly mean air temperatures during the warm period and the sum of negative monthly mean air temperatures during the cold period indicate that both the warm and the cold seasons warmed up by ca. 10% (Malkova et al., 2022).

From north to south Yamal Peninsula spans over three of the bioclimatic subzones of the Arctic defined in the circum-Arctic vegetation map (Walker et al., 2005). Each subzone covers approximately one third of the peninsula, starting from subzone C in the high Arctic, then subzones D and E (low Arctic) and finally reaching the forest-tundra ecotone located in the sub-Arctic (Figure 1). These subzones differ by their plant biomass, increasing from north to south, by their dominant plant species and by other characteristics of the vegetation, notably the presence of erect shrubs and willow

thickets (*Salix* spp.). The vegetation of subzone C consists mostly of graminoid, prostrate dwarf-shrub, forb tundra and prostrate/hemiprostrate dwarf-shrub tundra. It is dominated by sedges (*Carex* spp., *Eriophorum* spp.), and mosses (e.g., *Polytrichum* sp., *Sphagnum* sp.) and erect willows of at most 15 cm height. It has approximately 5%–50% cover of vascular plants with interrupted closed or patchy vegetation. In subzone D, the vegetation consists mainly of non-tussock sedge, dwarf-shrub, moss tundra and erect dwarf-shrub tundra. It is dominated by sedges, mosses and dwarf shrubs (*Dryas*, *Cassiope tetragona*, *Arctous rubra*, *Vaccinium* spp.), with willow thickets up to 40 cm high. Subzone E consists of a more complex mosaic of tussock-sedge, dwarf-shrub, moss tundra, erect dwarf-shrub tundra and low-shrub tundra. Willow thickets range mostly between one and two meters in height, but can in some places be higher and interspersed with alder (*Alnus* spp.). The vegetation is dominated by wild rosemary (*Ledum decumbens*), sedges, grasses, forbs, and sometimes thick moss carpets (*Sphagnum* spp., *Sanionia uncinata*). The forest tundra is characterized by the presence of trees (mostly Siberian larches, *Larix sibirica*), with quite dense forested areas especially south of the right bank of the Ob' river. Willow thickets here reach more than two meters in height. The vegetation is dominated by forbs, several species of sedges and mosses (e.g., *Mnium* sp., *Polytrichum* sp., *Sphagnum* sp.). Further details on the vegetation of Yamal can be found in Magomedova, Morozova, Ektova, Rebristaya, et al. (2006).

According to Korityn et al. (1995), there are nine species of small rodents in Yamal: Siberian lemming (*Lemmus sibiricus*), collared lemming (*Dicrostonyx torquatus*), narrow-headed vole, Middendorff's vole (*Alexandromys middendorffii*), northern red-backed vole (*Clethrionomys rutilus*), grey-sided vole (*Craseomys rufocanus*), tundra vole (*Alexandromys oeconomicus*), field vole (*Microtus agrestis*), and water vole (*Arvicola amphibius*). The number of species decreases from the south to the north of the peninsula. Other common vertebrate herbivores are the mountain hare (*Lepus timidus*), the willow (*Lagopus lagopus*) and rock (*Lagopus muta*) ptarmigan, domestic reindeer, and muskrat (*Ondatra zibethicus*) in the southern part of the peninsula.

The most common species are Siberian lemming, collared lemming, narrow-headed vole, Middendorff's vole, and northern red-backed vole (Sokolova et al., 2014). Both species of lemmings have Arctic distributions. The Siberian lemming occurs almost exclusively in low lying humid tundra and moss-dwarf birch tundra (Dunaeva, 1948; Sokolova, 2004). Sedges and mosses dominate its diet, but leaves and young shoots of dwarf birch, some willows, cloudberries, and horsetail (*Equisetum* spp.) are also consumed (Dunaeva, 1948; Kiryushchenko & Kiryushchenko, 1979; Kopein, 1958). Collared lemmings inhabit preferentially moss-dwarf birch tundra (Dunaeva, 1948; Sokolova, 2004). They feed on different types of deciduous and evergreen shrubs, but their diet also includes sedges, grasses, and forbs (Dunaeva, 1948). The narrow-headed vole is a widespread intrazonal species inhabiting river valleys and meadows from the steppe zone to the Arctic. In Yamal, it mostly occurs in flooded meadows, willow thickets and steep river

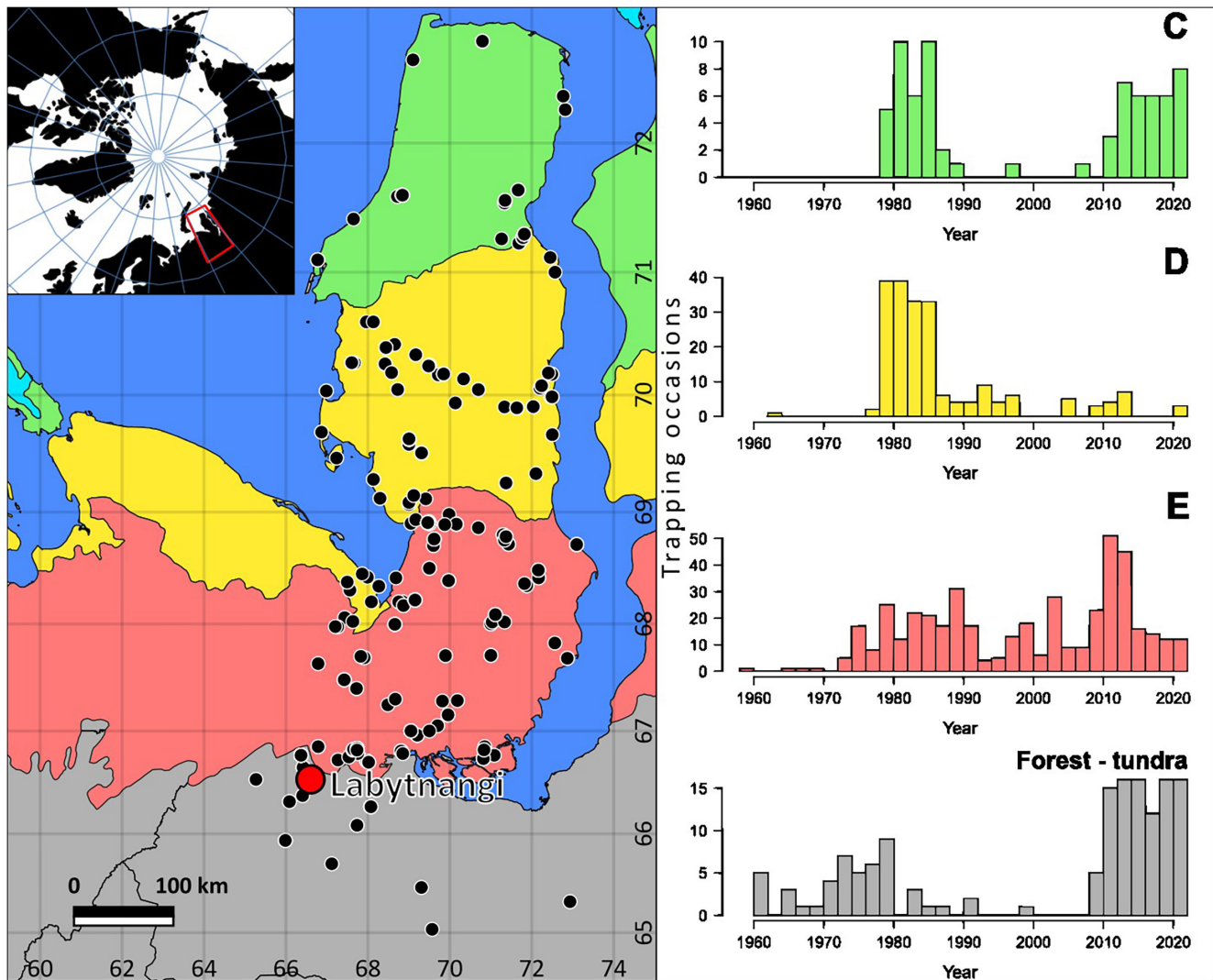


FIGURE 1 Left panel: Map of the Yamal Peninsula with all trapping locations. The insert shows the location of the study area in western Siberia. Colors indicate the bioclimatic subzones of the Circumpolar Arctic Region according to the circum-Arctic vegetation map (Walker et al., 2005) and the forest-tundra ecotone is shown in grey. Right panel: Temporal distribution of small rodent trapping occasions (see main text for definition) in each bioclimatic subzone and in the forest-tundra ecotone.

banks with lush vegetation (Dunaeva, 1948; Sokolova, 2004). The diet of narrow-headed voles consists of more than 40 species of sedges, grasses, forbs, and shrubs (Dunaeva, 1948; Kopein, 1958). The distribution of Middendorff's vole in western Siberia covers mostly the low-Arctic, including the northern part of the boreal zone, the forest-tundra and subzone E. It mainly inhabits lower laying humid tundra areas, often bogs characterized by mosses, dwarf birch and sedges (Dunaeva, 1948; Schwartz & Pyastolova, 1971; Sokolov & Sokolova, 2006). Its diet consists of the vegetative parts of forbs and graminoid plants, mainly sedges and cotton grasses (Schwartz & Pyastolova, 1971). The northern red-backed vole is primarily a boreal species but does occur in the low Arctic. In the tundra zone, it is mostly found in floodplains close to willow and alder thickets (Dunaeva, 1948). The basis of their diet consists of grasses, seeds of woody and herbaceous plants, berries, mushrooms, mosses, and lichens (Bangs, 1984; Flerov, 1933).

2.2 | Data on small rodents and statistical analyzes

The data included in the study all resulted from a single method—snap trapping, and were obtained from two sources: (a) Field work carried out by the authors in the period 1979–2022 and (b) data from other researchers working at the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences in Ekaterinburg (IPAE), that played a central role in ecological research on Yamal during the last half a century. These data spanned the years 1958–2008 and were either provided to us by the authors or published with the possibility to extract primary data. Two spatial designs to set up the snap-traps were used. The trap-line design that is classical in Russian zoology (Kucheruk, 1952) was used in 1958–2020. According to this design, lines of 50 or 100 traps are placed with intervals of 5 m along a line in a specific habitat. At each point, one trap is set up within a circle of 1 m diameter close to burrows of small rodents or on their

runways, if present. Traps are checked every 12 h and the duration of one session usually lasts 2–4 days (48–96 h). The small-quadrat design (Myllymäki et al., 1971) was used at three sites: Erkuta (subzone E) since 2007, Kharp (forest-tundra) since 2011 and Sabetta (subzone C) since 2014. According to this design, we placed three traps in a circle with a radius of 2 m around each corner of a 15 × 15 m quadrat (12 traps per quadrat) close to signs of small rodent activity, if present. Traps were checked once per day on two consecutive days. For 6 years (2010–2015) trapping was carried out at the same time according to both designs at Erkuta. As expected, the same species were detected (Fufachev et al., 2019), suggesting that the specific placement of the traps does not affect species detection. Some of the vole species occurring on Yamal are difficult to distinguish in the field. For these species, correct identification of all individuals was in most cases based on inspection of the patterns of their molars. In particular, all voles trapped north of their accepted distribution range were identified based on their molars. All trapping of small rodents was undertaken under the scientific plan of IPAE, and approved by its Bioethics Commission (protocol #014 dated 12/05/2023; https://ipae.uran.ru/information/bioethics_commission).

As the aim of our study was to assess changes in small rodent distribution and community composition over time, we aggregated the data to presence/absence of each species at each trapping occasion. We defined a trapping occasion as one trapping session carried out over a number of consecutive days in a specific habitat at one trapping site. A trapping site was defined as a study area where trapping was conducted. It could span from a few hundred square meters (one or two traplines), up to several square kilometers in a few extensive trapping sites. A spring and a fall trapping session in the same study area were thus considered two trapping occasions, and trapping in clearly distinct landscape strata (for instance meadows adjacent to willow thickets and mesic tundra) in the same session and study area was also considered separate trapping occasions, as the small rodent species have clearly distinct habitat preferences (Sokolova et al., 2014). At some sites, trapping was only carried out on one or a few occasions in the frame of large-scale surveys or short-term projects, whereas a few sites were long-term monitoring sites with repeated trapping over many years. Long-term data were available in particular for two sites: Erkuta in subzone E (68.22° E; 69.15° N; Figure 1) with trap line data from 1999 to 2006, 2010–2015 and bi-annual small quadrat data from 2007 to 2022 (in June and in August; Fufachev et al., 2019); and in Kharp in the forest tundra (66.77° E; 66.37° N) with bi-annual small quadrat data from 2011 to 2022 (in June and in September).

In order to assess changes in the occurrence of different small rodent species in each bioclimatic subzone over time, we applied generalized linear mixed models using Template Model Builder with a binomial error distribution (function *glmmTMB* of the package *glmmTMB* v1.1.2.3 in R; Magnusson et al., 2021). Because the data covered different time periods in each bioclimatic subzone, we created a separate model for each subzone. The response variable was presence/absence of the small rodent species at each trapping occasion. Fixed predictor variables were time and species, and the interaction

of these predictors. Trapping site (per habitat for the sites where trapping was carried out in several habitats in parallel) was included as a random effect in all models. This allowed us to estimate a trend in occurrence for each species in each subzone. If a species was captured less than 10 times in a subzone, we excluded it from the analysis as an estimated trend would have very high uncertainty. We also excluded species that occurred almost only in the forest-tundra ecotone, as Arctic small rodent communities were the main focus of our study. Model fit was assessed using the DHARMA package v0.4.5 in R (Hartig & Lohse, 2022). Marginal means of linear trends for each species in each subzone were estimated with the function *emmeans* of the package *emmeans* v1.8.5 in R (Lenth et al., 2023).

3 | RESULTS

Overall, we assembled small rodent trapping data on Yamal Peninsula going back to 1958. The total dataset comprised 861 trapping occasions. At 77 sites, trapping was carried only once (Figure S1), 17 sites had more than 10 trapping occasions and the most important study area, Erkuta, was represented with 228 trapping occasions over 25 years (several trapping sessions in several habitats each year). The data did not cover the same time period in the different bioclimatic subzones and included time gaps (Figure 1). For the forest-tundra, samples were obtained for 32 years since 1960; for subzone E, sampling represented 51 years since 1958; for subzone D, 24 years since 1978 and for subzone C, 21 years since 1980. The last year included in the dataset was 2022.

Overall, nine species of small rodents were captured, among which five were rather common over several bioclimatic subzones. The assembled data revealed changes in occurrence of these species in the subzones, and changes in the ranges of several species over the study period. Thus, Siberian lemmings were not detected recently in the two most southern subzones. The last individual of this species was caught in the forest tundra in 2000 and in subzone E in 2014, although in the 1970s and 1980s the species was regularly trapped there (Figure 2). Siberian lemmings are still common in subzone C, whereas for subzone D little data were collected during the last decade. The occurrence of collared lemmings was low in the forest-tundra during the whole period covered by the data. Even though this species was regularly captured there in the 1970s, only three individuals have been recorded since 1977 (in 2019, 2020 and 2022). North of the forest tundra, this species occurred regularly over the whole study period (Figure 2). Narrow-headed voles are at present distributed over the whole peninsula. However, this species was never recorded in subzone C before 2008 (Figure 2). Middendorff's vole occurred regularly in the forest tundra and in subzone E over the whole study period. In subzone D, it was recorded occasionally, but it was trapped for the first time in subzone C in 2015 and later in 2022, suggesting a northward expansion. Northern red-backed vole had the highest occurrence in the forest-tundra and was common in subzone E. In subzone D, it was trapped only two times (in 1985 and 1995) and it has never been recorded in subzone C.

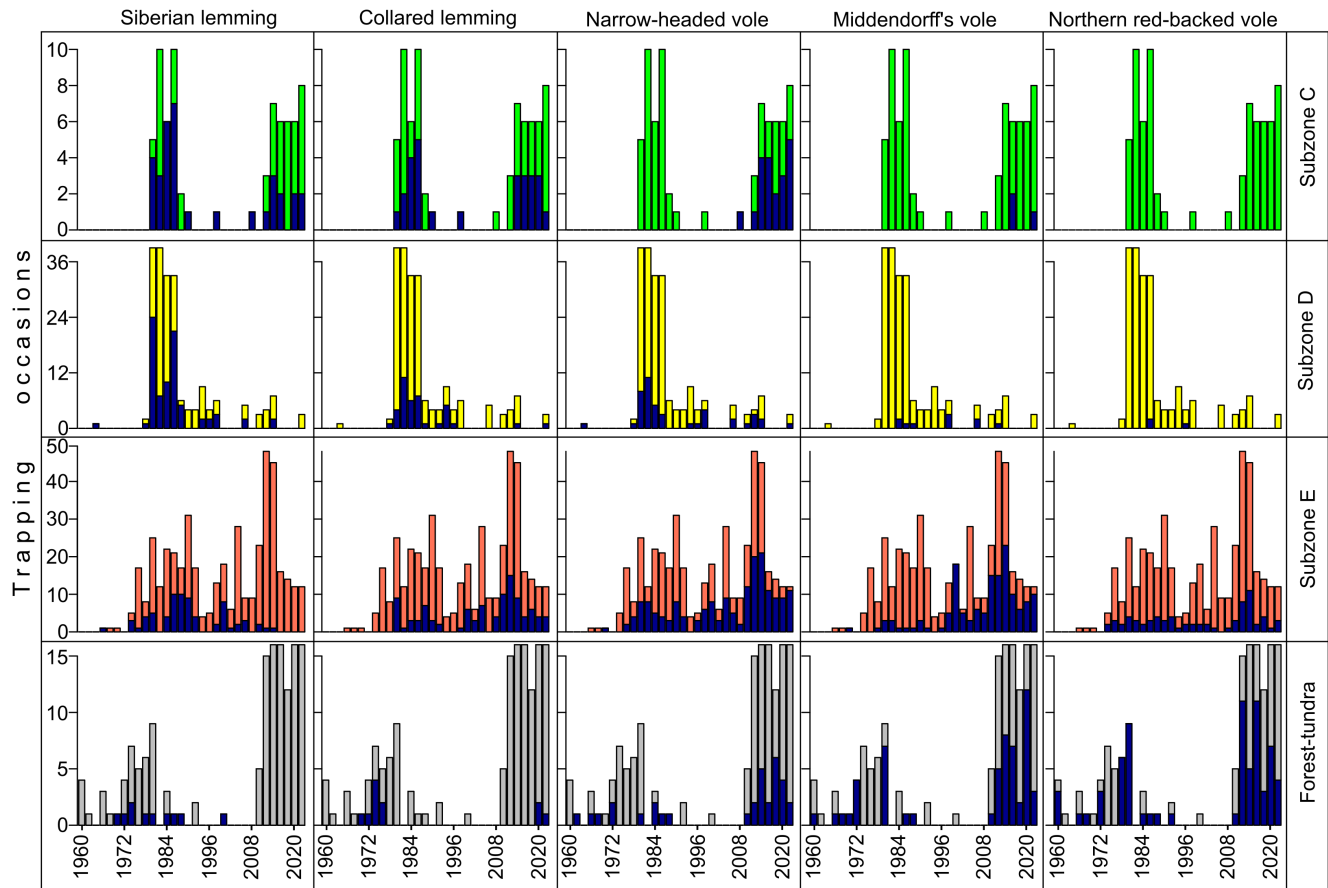


FIGURE 2 Occurrence of the five most common small rodent species from 1958 to 2022 in each of the three Arctic bioclimatic subzones of Yamal Peninsula (green—subzone C; yellow—subzone D; red—subzone E) and in the forest tundra ecotone (grey). The height of each bar shows the number of trapping occasions per year, with dark blue when the species was present and the rest of the bar representing the occasions when the species was absent.

Based on these data, we estimated trends of change in occurrence for each species in the different subzones over the study period. The occurrence of Siberian lemmings decreased over the study period in all four bioclimatic subzones (Figure 3; see Table S1 for model output and Table S2 for trend estimates). For collared lemmings, there was a negative trend in the forest tundra. In the Arctic bioclimatic subzones (C, D, E) however, we did not detect significant changes in occurrence of this species, and in subzone E the results even suggested a possible increase (Figure 3; Tables S1 and S2). Narrow-headed voles didn't show any significant trend in occurrence in the forest-tundra, but in the Arctic this species exhibited positive trends. For subzone D, the confidence interval of the estimate included 0, but for subzone C and E we found a significant increase in occurrence (Figure 3; Tables S1 and S2). For Middendorff's vole a positive trend in occurrence has been detected in the low Arctic (Subzones E and D). No trend could be estimated for this species in the high Arctic, but during the last 10 years it has also been trapped there (Figure 3). Finally, for northern red-backed voles a slightly negative trend of occurrence was detected for the forest-tundra and subzone E, but the confidence intervals of the estimates included 0 (Figure 3; Tables S1 and S2). For each species and

bioclimatic subzone, predicted probabilities of occurrence and the observed mean annual occurrences are shown in Figure S3.

In addition to these species, three species of voles were captured almost exclusively in the forest tundra: the grey-sided vole, field vole and tundra vole (Figure S2). All three were also recorded on rare occasions in the low Arctic subzone E. Finally, the water vole was captured on a few occasions in the forest tundra from 2015 onwards and trapped for the first time in subzone E in 2020 (Figure S2).

4 | DISCUSSION

The trapping data we assembled documented distribution patterns and occurrence trends of nine species of small rodents over more than 60 years in a latitudinal gradient from the forest tundra to the high Arctic. As predicted, we detected a decline in the occurrence of lemmings and an expansion of some vole species. In particular, the southern range limit of the Siberian lemming probably retreated north, out of the forest-tundra and maybe even subzone E. The occurrence of the collared lemming was more stable, and a significant decline was observed only in the forest tundra. At the same time,

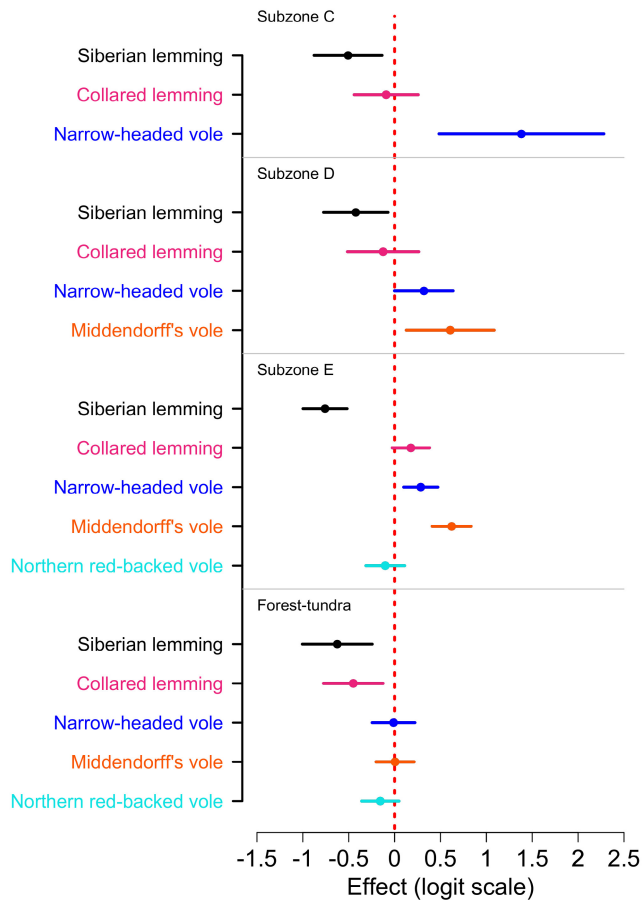


FIGURE 3 Marginal values of linear trends for changes in the occurrence of small rodent species with time in each bioclimatic subzones. The plot shows mean trends per decade on the logit scale with 95% confidence intervals.

we registered an expansion of the narrow-headed vole all the way to the north of Yamal Peninsula, and it is now the dominant species in trapping sessions also in the high Arctic. Its occurrence increased in all three tundra subzones. A similar pattern was detected for Middendorff's vole that also exhibited a significant increase in occurrence in the low Arctic subzones and was recently trapped for the first time in the high Arctic. Moreover, the water vole, a primarily boreal and temperate species, was for the first time caught in snap traps in subzone E in 2020. This species is significantly larger than the other small rodents and snap traps are thus not an optimal method to monitor it. However, the occurrences reported here for 2020 represent a considerable northwards advance relative to previous records from Yamal: since the 1970s water voles were caught repeatedly by other methods up to the border between the forest-tundra ecotone and the low Arctic, ca 150km further south (V. F. Sosin, unpublished field notes).

Considering its spatiotemporal extent, our dataset is particularly valuable because it consists of data collected over an important climatic gradient over time (despite some gaps), and not only of two separate points in time (Craig et al., 2020; Moritz et al., 2008). Moreover, it is based on a single method—snap trapping—that was

carried out according to only two standardized spatial trapping designs (trap-lines and small quadrats). Different sampling methods for small rodents have indeed been shown to provide contrasting results regarding species composition and structure of small mammal communities in some studies (Rocha et al., 2023). Other large-scale compilations of small rodent data had to deal with considerably higher heterogeneity of methods (e.g., Cornulier et al., 2013; Ehrich et al., 2020). In our dataset, an important source of variability was due to the temporal structure of the data. Lemmings and northern voles are well known for their multi-annual population cycles with a period of 3–5 years (e.g., Balakhonov et al., 1997; for Yamal; Stenseth, 1999). Long-term surveys would thus optimally consist in time series data collected with the same protocol at the same site and same time of the year. Such data would also allow addressing trends in abundance (e.g., Wan et al., 2022). Only a small part of our data consisted however of time series, and many data points came from locations where small rodents were trapped only once or over a few years. In the latter case, the chance to detect a species will strongly depend on the unknown phase of the cycle determining the abundance at the time when the trapping was carried out. The probability of species detection increases indeed with species abundance (Palmeirim et al., 2020). Although sampling effort (number of trap nights) affects species detectability (Moritz et al., 2008), as well as some times the exact model of snap traps used (Jung & Pretzlaw, 2022), in our data the variation resulting from different phases of the small rodent cycle was likely by far the most important. Analyzing our data as raw presence/absence data we assume that the heterogeneity arising from these temporal fluctuations, which occur on a much shorter time scale (seasonal or 3–5 years) than the trends we address, will primarily result in more noise in the data, but not in a systematic bias.

Given the different sources of variability in detectability addressed above, our data do not reflect the true distributions of the species as other methods would be required to document absence (Moritz et al., 2008). Thus, it is probably still possible to trap for example Siberian lemmings somewhere in southern subzones in some years. However, the fact that the data revealed both positive and negative trends in occurrence for different species in different bioclimatic subzones, makes it unlikely that they were impacted by a systematic bias. Moreover, the trends we documented in subzone E were in accordance with trends in abundance indices determined at the site with the longest time series, Erkuta. Here, a clear decrease in the abundance of lemmings, in particular Siberian lemmings, and an increase in narrow-headed voles was observed (Ehrich et al., 2020; Fufachev et al., 2019). When a species declines to a level where it only occurs at very low abundance, it loses its ecological functions. Thus, lemmings do not support specialized predators in southern Yamal any more (Ehrich et al., 2017; Fufachev et al., 2019), and it is likely that they do not exert major roles as grazers any more either (Baubin et al., 2016). Therefore, we are confident that the changes in occurrence that are documented in the data we assembled reflect real and ecologically important changes in the small rodent communities in different tundra subzones of Yamal. In the following we discuss possible drivers for the documented changes.

The observed decline in the occurrence of lemmings is likely to be related to changes in winter climate. Winter climate and the physical properties of the snowpack are indeed crucial conditions for small rodents and especially for lemmings, that not only live a substantial amount of time in the subnivean space, but also regularly breed under the snow (Koshkina & Khalanski, 1962; Krebs, 1964). A negative relationship between hardness of basal snow layers and lemming population growth was documented both for lemmings in the high Arctic (Domine et al., 2018) and in the Fennoscandian mountain tundra (Kausrud et al., 2008). Moreover, based on empirical data from Greenland, the demography of lemming populations (*Dicrostonyx groenlandicus*) was modeled under effects of climate change (Gilig et al., 2009). All likely scenarios, notably increased frequency of melt-freeze events and elongation of the snow-free period, increased the length of the lemming population cycles and decreased their maximum densities.

In Yamal, in particular in the southern part of the peninsula, it is likely that freeze-thaw episodes in winter have become more frequent, as in other areas of the Arctic (Boisvert & Stroeve, 2015; Liston & Hiemstra, 2011; Peeters et al., 2019), and several important regional rain-on-snow events have been described (Bartsch et al., 2010, 2022; Sokolov et al., 2016). Thus, milder winters with harder snow are likely to have contributed to the observed general decline in Siberian lemmings. Interestingly, according to our data, collared lemmings seemed less affected and their occurrence declined significantly only in the forest tundra. This difference is in agreement with the results of Poirier et al. (2021) showing that nearctic collared lemmings (*D. groenlandicus*) were more efficient in digging through hard snow than brown lemmings (*Lemmus trimucronatus*). This is most probably because collared lemmings develop large claws on their front legs in early winter unlike brown lemmings (Hansen, 1957). Differences in winter habitat may also have contributed to the different trends observed for the two lemming species on Yamal. While the winter habitat of Siberian lemmings is in fertile open fens, collared lemmings in the low arctic prefer snow beds on steep slopes with dwarf birches (Dunaeva, 1948), a habitat where snow is likely to remain looser. Contrary to the lemmings, the occurrence of voles was in general increasing or stable, suggesting that in Yamal they are not at the moment negatively affected by ongoing changes in winter climate.

Voies of the tribe Microtini, including both the narrow-headed vole and Middendorff's vole feed on grasses and forbs. Their increased occurrence may have been favored by increased growth of forbs and grasses, which might be driven by longer and warmer summers in the Arctic (Bjorkman et al., 2020; Elmendorf et al., 2015). Epstein et al. (2020) recently documented a positive relationship between the summer warmth index and plant biomass along a large-scale transect over Yamal. Hence, ongoing warming could potentially have a positive effect on both plant species diversity and biomass towards the north of the peninsula, and vegetation dominated by grasses and forbs might replace to some degree the low productive moss dominated habitats typical for subzones D and C which are suitable for Siberian lemmings. Moreover, a recent study shows a

northward shift of 50–100 km of the boundary between the high and the low Arctic on Yamal (Ermokhina et al., 2023).

Such vegetation changes potentially increasing the habitat of voles at the expense of lemming habitat might be enhanced by the impact of intensive reindeer herding and industrial development. Reindeer have been shown to affect tundra vegetation through grazing, browsing, trampling and fertilizing (Heggenes et al., 2017; Tuomi et al., 2021). All these impacts are able to change plant communities towards higher productivity and a dominance of graminoids (Egelkraut et al., 2018; Olofsson et al., 2004). During the time covered by our study, the number of reindeer on Yamal Peninsula (ca. 122,000 km²) more than doubled from ca. 100,000 in 1960 (Makeev et al., 2014) to officially over 225,000 animals today (FAO, 2022). Several studies show that reindeer herding is the most important driver of vegetation change in Yamal leading to damage or even complete destruction of the lichen cover, inhibition of shrub expansion and promotion of secondary graminoid dominated vegetation communities (Forbes et al., 2009; Kryazhimskiy et al., 2011; Spiegel et al., 2023).

A similar vegetation transition towards more graminoid dominated communities favorable for voles can be expected to result locally from the environmental impact of industrial development. According to some estimations, Yamal peninsula has the highest rates of hydrocarbon development in the Arctic (Shchegolkova, 2021). Associated mechanical disturbance of the soil, vegetation, and hydrological regime, lead to geo-ecological changes in the local landscape (Raynolds et al., 2014; Walker et al., 2011; Bogdanov et al., 1997) and promote rather simple graminoid dominated habitats with relatively dense grass swards (Magomedova, Morozova, & Ektova, 2006; Morozova et al., 1995). Another reason for the spreading of grass dominated habitats around man-made objects is the revegetation of sand quarries, roadsides, and the area around other infrastructure objects through sowing of grass mixtures dominated by the seeds of perennial graminoids (Skipin et al., 2014; Tyuryukov, 2019).

The conspicuous northward expansion of the narrow-headed vole may also be hypothesized to be related to willow shrub expansion. Among the small rodent species of Yamal, this species indeed prefers willow thickets to other biotopes (Dunaeva, 1948; Sokolova et al., 2014). Longer and warmer summers have been shown to enhance growth and northward expansion of willows thickets in several areas of the Arctic (Mekonnen et al., 2021; Myers-Smith et al., 2011). This has contributed to spreading of birds and mammals closely related to willow thickets as their primary habitat (Sokolov et al., 2012; Zhou et al., 2017). The indigenous Nenets people living in Yamal report an overall trend of expansion and increased growth of erect shrubs on the peninsula (Forbes & Stammer, 2009). Moreover, during our trapping in subzone C (71.41° N, 67.58° E), the reindeer herder Rodion Serotetto (personal communication) told us that “recently a new mouse species appeared that had tails” (meaning voles compared to the mice he was used to, lemmings, which have very short tails). He also said that there were only lemmings in this area when he was young, and that he believes that these “new mice” most probably followed the expanding shrubs in the area.

5 | CONCLUSION

The revealed decline in occurrence of lemmings, native to the Arctic, and increase of more widespread voles in Yamal peninsula is consistent with borealization of the tundra zone of this part of the Arctic during last 60 years. The changes we observed are coherent with the expected impact of ongoing ecosystem changes as outlined above, however the available data did not allow for a formal analysis of the specific effect of different hypothesized drivers. Determining the causes of the documented changes in small rodent communities will require targeted ecosystem-based monitoring allowing to directly relate hypothesized drivers of change to ecological state variables (Lindenmayer & Likens, 2009). Independent of their causes, the observed changes will have important consequences for the functioning of this tundra ecosystem, affecting both plants and importantly specialized Arctic predators that depend on lemmings to reproduce.

AUTHOR CONTRIBUTIONS

Natalia A. Sokolova: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing. **Ivan A. Fufachev:** Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – review and editing. **Dorothee Ehrich:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; resources; supervision; visualization; writing – review and editing. **Victor G. Shtro:** Conceptualization; data curation; investigation; methodology; resources. **Vasiliy A. Sokolov:** Funding acquisition; investigation; writing – review and editing. **Aleksandr A. Sokolov:** Conceptualization; funding acquisition; investigation; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Dryad at <https://doi.org/10.5061/dryad.3ffbg79rb>.

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