

Long-term changes of small mammal communities in heterogenous landscapes of Central Europe

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Abstract Long-term dynamics of small mammal communities are perennial themes in population ecology. However, comprehensive studies on the effect of environmental factors on population dynamics are still rare. Here, we aimed to analyze long-term data on Central European communities of small mammals occurring in two habitats that greatly differed in their structure, successional stages, and forest management. We found a richer community structure in young spruce plantations compared to mature European beech forests. In young spruce plantations, *Myodes glareolus* and *Apodemus flavicollis* abundances increased and *Sorex araneus* abundances decreased during the study period as a result of forest growth and management. Community structure in mature beech forests did not change significantly during the study period. *Apodemus flavicollis* and *Myodes glareolus* showed 3- and 5-year population cycles, respectively, and their abundances were simultaneously positively correlated with relative abundance of masts. Weather also played a role, while the effect of snow cover was pronounced only in mountain areas where it negatively affected *Microtus agrestis* and *Sorex*

araneus abundances, temperature positively and rainfall negatively influenced *Myodes glareolus* and *Apodemus flavicollis* abundances across both studied habitats. Our findings document that a complex of environmental factors significantly affects the structure and dynamics of small mammal communities in Central Europe, and both local biotic and abiotic factors should be considered in future studies.

Keywords Habitat diversity · Population dynamics · Community structure · Small mammal · Temperate area · Weather · Masting

Introduction

Small herbivorous, granivorous, and insectivorous species of mammals represent an important part of terrestrial ecosystems; in particular, they serve as a prey for various avian and mammalian predators (Newton 1979; Zárbybnická et al. 2015a) and influence forest management, especially with regard to voles which can periodically cause extensive damage to tree seedlings (e.g., Lyly et al. 2014). Distribution of small mammals is non-random as a result of individual selection for suitable habitats and is affected mainly by the distribution of food resources, shelter availability, and the abundance of conspecifics (Krebs 2013). According to the habitat-heterogeneity hypothesis, an increase in the number of different habitats usually leads to an increase in species diversity (MacArthur and MacArthur 1961). The hypothesis gained support in studies from both successional (Bollinger 1995) and disturbed environments (Krojerová-Prokešová et al. 2016), as well as along latitudinal (Willig et al. 2003), altitudinal (Finch 1989), and humidity gradients (Daniels et al. 1992). For example, the presence of small-sized clearings in compact Central European forests (Krojerová-Prokešová et al. 2016)

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or successional habitats disturbed by fire events in Brazilian savannas (Briani et al. 2004) may be important for the maintenance of high diversity in small mammal communities.

The abundances of small mammal populations vary temporally and spatially, as a result of exposure to a wide range of biotic and abiotic factors. In particular, seasonal and between-year population changes may be driven by environmental factors (e.g., latitude, day-length, temperature, plant productivity, weather), biotic factors (e.g., predation), and intrinsic factors (e.g., pathogens) (Krebs 2009, 2013). The regular 3–4-year cycles with low, increasing, peak and decreasing population phases are typical for voles at higher latitudes (e.g., Hanski et al. 1991; Korpimäki et al. 2005). The abundances of their counterparts at lower latitudes are relatively stable both within and between years (Hanski et al. 1991; Hansson and Henttonen 1985), although it is not a general rule (Tkadlec and Stenseth 2001). In recent decades, vole population cycles can show a pattern of dampened amplitudes, as a possible result of climate changes (Cornulier et al. 2013; Gouveia et al. 2015), but this pattern probably does not function globally (Korpela et al. 2014). Despite numerous studies investigating the structure of small mammal communities and their temporal changes, there is still little progress in piecing together the puzzle of rodent population dynamics, mainly because the time series are often too short (Berryman 2002; Zub et al. 2012).

We studied the structure and population dynamics of Central European small mammal communities in different habitats (i.e., young spruce plantations and mature European beech forests) in relation to climatic conditions and food availability during the period 1997–2015 and 2001–2015, respectively, as well as the effect of habitat changes in young spruce plantations on community structure during the period 1991–2015. In particular, we expected (i) richer community structure and more pronounced fluctuating dynamics of small mammal populations would be found in habitats of early successional stages (i.e., young spruce plantations) compared to old-growth habitats (i.e., mature beech forests), (ii) cyclicity would be more clearly pronounced in voles than other small mammal species (mice and shrews), and (iii) effects of climatic conditions and food availability on small mammal dynamics would follow the life strategy of particular small mammal species in each habitat.

Methods

Study area

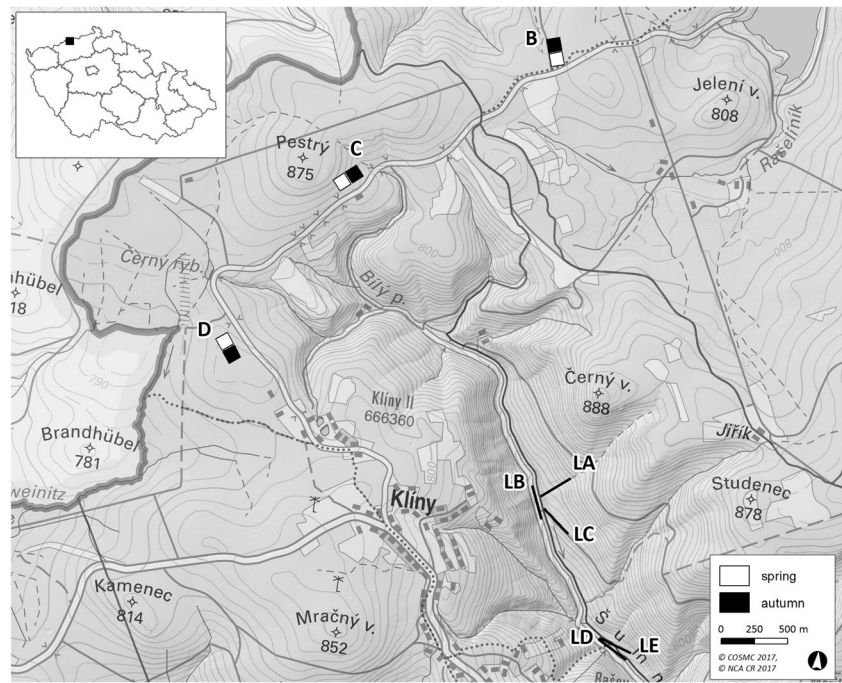
The study area was situated in the northern part of the Czech Republic (50.7° N, 13.6° E) close to the border with Saxony (Germany), in the Ore Mountains (Krušné hory in Czech). The area has a sharp increase in elevation from 300 m a. s. l. (the town of Litvínov) to 960 m a. s. l. (Mt. Loučná) over a distance of 7 km, i.e., an elevation gradient of ca. 100 m/km.

During the second half of the twentieth century, the Ore Mountain plateau was characterized by intensive air pollution from industry and power plants located in the foothills and high air deposition of metallic elements (Sucharová and Suchara 1998). This resulted in massive destruction of Norway spruce (*Picea abies*) forests on the mountain plateaux, being followed by intensive logging of dead trees and the consequent restoration with native (mainly birches *Betula* sp., European mountain ash *Sorbus aucuparia*, and European larch *Larix decidua*) and non-native trees (blue spruce *Picea pungens*) (Kopáček and Veselý 2005; Zárbynická et al. 2015b). The extensive blue spruce plantations have been substituted with native Norway spruce seedlings in the past decade.

Trapping procedure and habitat description

Small mammals were collected using snap-traps in two trapping areas with different habitats. The first (young spruce plantations) was located on the mountain plateau in clear-cuts at 820–860 m a.s.l. during the period 1991–2015. In this area, three 1-ha trapping squares (designated B, C, and D) were situated at a distance of 1.6 to 1.8 km from each other. In each square, a grid of 11 × 11 traps, 10 m apart, was laid (totalling 121 traps per trapping square) (methodology based on Pelikán 1975). To eliminate the negative effect of catching individuals within 1-ha squares on consequent trappings at the same locality, we situated autumn traps in a neighboring area. Thus, spring and autumn trapping sites (B, C, D) did not overlap (Fig. 1). The habitat structure of trapping squares varied considerably due to the successional process and forest management. We used vegetation maps originally developed for the purposes of the Forestry Institute of the Czech Republic (Forest Management Plans, 1:10,000 m) to quantify these changes. These maps described the actual habitat structure for given years (i.e., 1991, 2001, and 2011). Based on the vegetation maps, we divided the study period into three 5-year periods (1991–1995, 2001–2005, 2011–2015), and defined the height layers (< 1, 1–6, 6–10, > 10 m) and the relative abundance (%) of tree species (blue spruce, Norway spruce, European beech *Fagus sylvatica*, European larch, European mountain ash, silver birch *Betula pendula*, mountain pine *Pinus mugo*, sycamore *Acer pseudoplatanus*) in each height layer, time period, and trapping square. The habitat of these trapping squares was dominated by blue spruce and birch seedlings in the early successional stage (years 1991–1995), by blue spruce at 1–6-m height in the middle successional stage (years 2001–2005), and by blue spruce at above 10-m height and Norway spruce seedlings up to 1 m in the late successional stages (years 2011–2015) (Table 1). The vegetation undergrowth was dominated by a dense canopy of hairy reed grass (*Calamagrostis villosa*) throughout the whole study period. The ground was covered by numerous root balls and coarse woody debris as a result of the logging and restoration processes.

Fig. 1 The distribution of trapping squares and trapping lines in the Ore Mountains, Czech Republic



The second trapping area, at a distance of 3 km from the first one, was situated at the foot of the mountains in 200-year-old beech forests at an elevation of 450–500 m (i.e., mature beech forests) during the period 1997–2015. This site was characterized by high sloping and undulation with a mosaic of streams, roads, and paths. This habitat was not suitable for the installation of a 1-ha trapping square. In this habitat, five trapping lines, each 250 m long (designated LA, LB, LC, LD, and LE), were situated within a distance of 50–1500 m from each other (methodology based on Pelikán 1975). A total of 50 traps, spaced within 5 m of each other, were laid in each line. The habitat was dominated by European beech (*Fagus sylvatica*, more than 90%) without significant forest management during the

whole period. The ground underneath was covered with low and sparse herbal vegetation (e.g., wood sorrel *Oxalis acetosella*, arctic starflower *Trientalis europaea*), and with leaf litter.

Traps were exposed every spring (at the beginning of June) and every autumn (at the beginning of October) in both trapping areas. The traps were baited with flour roasted on bacon, left effective for 3 days, and checked every morning. The abundance of small mammals was calculated as the number of captured individuals per 100 trap nights in each trapping square and line, respectively. The relative abundance was determined as the proportion (%) of individual species in the sample. All captured mammals ($n = 4172$) were identified to species level.

Table 1 Relative abundance (%) of tree species in each height layer (1, < 1 m; 2, 1–6 m; 3, 6–10 m; 4, > 10 m), time period (1991–1995, 2001–2005, 2011–2015), and trapping square (B, C, D) in young spruce plantations based on forest vegetation maps. Sum for each layer is 100%

Time period	1991–1995				2001–2005				2011–2015								
	B	C			D	B	C			D	B	C					
Trapping square	B	C			D	B	C			D	B	C					
Height layer	1	2	3	4	1	1	2	2	3	4	2	2	3	1	4	1	3
<i>Fagus sylvatica</i>												15					15
<i>Betula pendula</i>		60	10		20			60	10		20				5		5
<i>Sorbus aucuparia</i>					15						15	5		15		10	10
<i>Acer pseudoplatanus</i>						80						10					
<i>Pinus mugo</i>	5				5		5				5						10
<i>Larix decidua</i>	20				15	10	20				15	15	15				15
<i>Picea abies</i>				100						100		40		85	10	75	
<i>Picea pungens</i>	75	40	90		45	10	75	40	90		45	15	85		85		60

We found that community structure (expressed by percentages of each species) and abundances (the number of caught individuals per 100 trap nights of each species) significantly differed among trapping lines in mature beech forests and trapping squares in young spruce plantations, respectively (correspondence analyses, Canoco 5 software: abundances in mature beech forests: pseudo- $F = 3.7$, $p = 0.045$; structure of community in mature beech forests: pseudo- $F = 10.4$, $p = 0.002$; abundances in young spruce plantations: pseudo- $F = 3.1$, $p = 0.020$; structure of community in young spruce plantations: pseudo- $F = 2.8$, $p = 0.022$, percentages were arcsine transformed, p values were obtained by Monte Carlo permutation tests, random factors were spring/autumn period and year). Therefore, we used trapping square/line and period (spring/autumn) as random factors in the analyses (see below).

Statistical analyses

Species diversity of the small mammal community in each habitat was calculated using the Shannon-Wiener diversity index (Krebs 2009). Changes in vegetation structure at three trapping squares in young spruce plantations were visualized by principal component analysis (PCA) using Canoco 5 software (ter Braak and Šmilauer 2012). Response variables were represented by arcsine-transformed relative abundances of each tree species for the relevant 5-year period (1991–1995, 2001–2005, 2010–2015), trapping square ($n = 3$), and height layer (< 1, 1–6, 6–10, > 10 m). Height layers and 5-year periods were used as supplementary variables and were passively projected into the ordination space. Changes of vegetation structure in mature beech forests during our study were negligible and were not used in further analyses on the effect of habitat change on small mammal community structure.

Using redundancy analyses (RDA) in Canoco 5 software (ter Braak and Šmilauer 2012), we assessed the effect of habitat changes on small mammal community structure between the 5-year periods (1991–1995, 2001–2005, 2010–2015) in young spruce plantations. These analyses were performed separately for spring and autumn data. The data unit was represented by the abundance of individual small mammal species (i.e., field vole *Microtus agrestis*, bank vole *Myodes glareolus*, yellow-necked mouse *Apodemus flavicollis*, common shrew *Sorex araneus*, and other rare species that were pooled in the group “others”) obtained at each trapping square/line in each year. The analyses were performed only on the basis of the pooled data from each 5-year period. The data unit was represented by relative abundances of individual small mammal species at each trapping square and 5-year period ($n = 9$ samples) which were arcsine transformed prior to analyses. Relative abundances of each tree species within each height layer ($n = 32$ factors) were used as explanatory variables, and 5-year period as a supplementary variable. We used forward selection of explanatory variables based on AIC

criterion, and statistical significances were obtained by Monte Carlo permutation tests.

Data for the purposes of the following analyses were collected during the period 1997–2015. The cyclicity of small mammal abundances was checked using the autocorrelation function in Statistica 12 software (StatSoft 2013). These analyses were performed for spring and autumn and for each habitat and small mammal species separately. The data unit was represented by mean annual abundances obtained at trapping squares/lines ($n = 19$ samples). Only significant results are shown.

Long-term changes in abundances of the four most dominant species (yellow-necked mouse, bank vole, field vole, and common shrew) were analyzed using quasi-likelihood GLMM models in R software version 3.14. We used the pooled dataset from spring and autumn abundance per 100 trap nights of each species (dependent variables). These analyses were performed for each habitat separately ($n = 114$ trappings at three trapping squares, $n = 190$ trappings at five trapping lines). Trapping square/line and period (spring/autumn) were used as random factors. We also used the abundance of yellow-necked mouse 3 years ago and the abundance of bank vole 5 years ago as covariates to consider known population dynamics of these species in the study area. Factor year was used as a continuous independent variable. For each species, we compared the null model (with random factors only) with the model where the factor year was added.

The effect of weather and trapping period on abundances of the four most abundant species was analyzed by GLMM in R software version 3.14 using quasi-likelihood models. These analyses were performed separately for each species (yellow-necked mouse, bank vole, field vole, and common shrew) and separately for young spruce plantations ($n = 114$ trappings at three trapping squares) and mature beech forest ($n = 190$ trappings at five trapping lines). In all analyses, we used locality (trapping line/square) and year as random factors. We also used the abundance of yellow-necked mouse 3 years ago and the abundance of bank vole 5 years ago as covariates. Dependent variables were represented by abundances of each species per 100 trap nights. We used trapping period (spring/autumn), mean monthly rainfalls in actual and previous spring (February–May) and summer (June–September), mean monthly temperature in actual and previous spring and summer, and mean monthly (November–April) maximal snow cover in the previous winter and the winter before as independent variables. Factors were added to the null model based on AIC criterion using forward selection. We showed only significant results. Data on weather conditions were obtained from the Czech Hydrometeorological Institute stations in close vicinity of the study area.

Data on masting were collected on 20 randomly distributed plots (each plot covered 0.25 m²) in the forest canopy every early October during the period 2000–2015. Due to the

difference in time of data gathering, we calculated its effect (independent variable) on species abundances (dependent variables) separately. Relationships between mean yearly spring and autumn abundances of granivorous species, i.e., bank vole and yellow-necked mouse, in the period 2001–2015 and masting in the previous year (2000–2014) were calculated for each habitat and period separately using GLMM in R software version 3.14 using quasi-likelihood models. We also used the abundance of yellow-necked mouse 3 years ago and the abundance of bank vole 5 years ago as covariates. The relative abundance index of masting (0–3) for each year was calculated based on the number of nuts per square meter.

Results

Community structure

We caught 1663 small mammal individuals using the square method in young spruce plantations and 2509 individuals using the line method in mature beech forests during the period 1997–2015 (Table 2). In the pooled dataset ($n = 4172$), yellow-necked mouse (42.2%) was the dominant species, followed by bank vole (34.6%), field vole (11.3%), and common shrew (8.1%). Other species comprised less than 4.0% (Table 2). The Shannon index was 1.72 for young spruce plantations, and 1.08 for mature beech forests. Small mammal communities differed between the

habitats; field vole, bank vole, yellow-necked mouse, and common shrew dominated in young spruce plantations, whereas only yellownecked mouse and bank vole dominated in mature beech forests (Table 2).

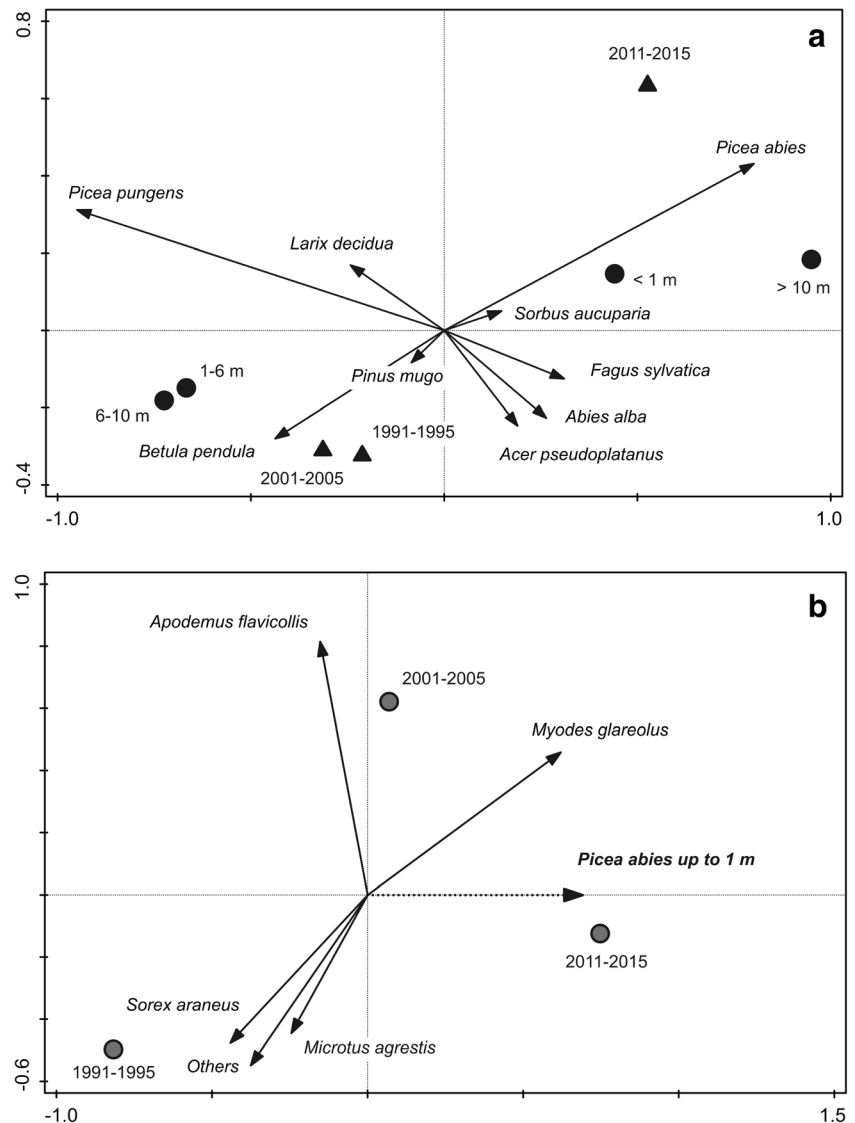
The effect of habitat structure

We found no changes in habitat structure in mature beech forests during the study period. Substantial changes occurred in young spruce plantations as a consequence of management measures. These habitats were not dominated by any tree species during the first (1991–1995) and second (2001–2005) 5-year periods, but young Norway spruce up to 1-m height became a dominant tree during the third period (2011–2015) (Fig. 2a). We found a significant effect of habitat changes on the structure of the autumn small mammal community (RDA analysis, I and II ordination axes explained 72.5% of variability, pseudo- $F = 6.4, p = 0.020$, Fig. 2b). In particular, we found a positive effect of the representation of young Norway spruce (correlation coefficient with first ordination axis 0.97) on the relative abundance of bank vole in autumn (0.75), a negative effect on the relative abundance of field vole (− 0.35), common shrew (− 0.57), and other species (− 0.55) in autumn, and no pronounced effect on the relative abundance of yellow-necked mouse in autumn (− 0.11, Fig. 2b). The spring community structure was not affected by this habitat development (RDA, I and II ordination axes explained 45.0% of variability, pseudo- $F = 2.3, p = 0.090$).

Table 2 Numbers and relative abundances (%) of small mammal species in young spruce plantations and mature beech forests during the period 1997–2015

Species	Young spruce plantations						Mature beech forests						Total	
	Total		Spring		Autumn		Total		Spring		Autumn		n	%
	n	%	n	%	n	%	n	%	n	%	n	%		
<i>Apodemus flavicollis</i>	387	23.2	214	37.5	173	15.8	1373	54.7	921	59.1	452	47.5	1760	42.2
<i>Apodemus sylvaticus</i>	6	0.4	3	0.5	3	0.3	6	0.2	2	0.1	4	0.4	12	0.3
<i>Arvicola terrestris</i>	1	0.1	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	1	0.0
<i>Myodes glareolus</i>	414	24.8	106	18.5	308	28.2	1031	41.1	577	37.1	454	47.7	1445	34.7
<i>Crocidura leucodon</i>	1	0.1	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0	1	0.0
<i>Micromys minutus</i>	2	0.1	0	0.0	2	0.2	0	0.0	0	0.0	0	0.0	2	0.0
<i>Microtus agrestis</i>	440	26.4	177	31.0	263	24.1	31	1.2	20	1.3	11	1.2	471	11.3
<i>Microtus arvalis</i>	51	3.1	6	1.1	45	4.1	7	0.3	5	0.3	2	0.2	58	1.4
<i>Microtus subterraneus</i>	11	0.7	6	1.1	5	0.4	11	0.4	7	0.4	4	0.4	22	0.5
<i>Muscardinus avellanarius</i>	0	0.0	0	0.0	0	0.0	6	0.3	4	0.3	2	0.2	6	0.1
<i>Neomys fodiens</i>	0	0.0	0	0.0	0	0.0	3	0.1	0	0.0	3	0.3	3	0.1
<i>Sorex araneus</i>	302	18.2	51	8.9	251	23.0	35	1.4	20	1.3	15	1.6	337	8.1
<i>Sorex minutus</i>	47	2.8	7	1.2	40	3.7	6	0.3	1	0.1	5	0.5	53	1.3
<i>Talpa europaea</i>	1	0.1	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0	1	0.0
Total	1663	100	571	100	1092	100	2509	100	1557	100	952	100	4172	100

Fig. 2 Changes in **a** habitat structure during the three 5-year periods (1991–1995, 2001–2005, 2011–2015) and **b** small mammal community structure related to the relative abundance of *Picea abies* during the three 5-year periods (1991–1995, 2001–2005, 2011–2015). Relative abundances (%) were used



Long-term population trends

We recorded significant changes in the abundance of all four most abundant species in young spruce plantations (GLMM analyses, Table 3). We recorded a long-term increase in the relative abundance of yellow-necked mouse (Fig. 3a) and bank vole (Fig. 3b) and long-term decrease in the abundance of common shrew (Fig. 3c). Abundances of field vole did not change significantly during the study period (Table 3). We did not record significant effects of year on abundances of small mammals in mature beech forests (GLMMs, p at least 0.290).

Population cycles

We found significant 3-year population cycles only in yellow-necked mouse in young spruce plantations among successive springs (Fig. 4a). These cycles became pronounced after the

year 2000, with clear peaks in 2004, 2007, 2010, 2012, and 2015 (Fig. 4c). We further found significant 5-year cycles in bank vole in mature beech forests among successive autumns (a 5-year cycle was also significant in successive springs, $p = 0.030$, but the correlation coefficient did not reach the confidence interval), with 2- and 3-year cycles also indicative among successive autumns ($p = 0.080$ and 0.090 , respectively) (Fig. 4b, d).

The effect of weather, food, and trapping period

Weather significantly affected the abundances of all four most abundant small mammal species, but effects of weather factors differed considerably between species (Table 3). Temperature in the previous spring and summer positively influenced abundances of yellow-necked mouse and bank vole in mature beech forests (Fig. 5a) and abundances of yellow-necked mouse in young spruce forests, respectively (Fig. 5c).

Table 3 The effect of factors to the abundances of the four most often caught small mammal species (expressed as the number of individuals per 100 trap nights) in young spruce plantations and mature beech forests during the period 1997–2015 in the Ore Mountains, Czech Republic. GLMM analyses. NA, not applicable

Habitat	Dependent variable	Independent variable	df	% of explained variability	Beta	Chi	p
Mature beech forests	<i>Apodemus flavicollis</i>	Temperature in previous spring	185	1.5	0.68	18.3	< 0.001
		Period (spring/autumn)	184	0.9	NA	11.1	< 0.001
	<i>Myodes glareolus</i>	Rainfall in previous summer	183	0.8	- 0.90	9.2	0.002
		Temperature in previous spring	182	0.6	0.60	6.9	0.009
Young spruce plantations	<i>Apodemus flavicollis</i>	Temperature in previous summer	111	9.0	0.99	35.8	< 0.001
		Rainfall in previous summer	110	2.0	- 0.64	8.1	0.005
	<i>Microtus agrestis</i>	Snow cover in winter	112	1.8	- 0.91	8.9	0.003
	<i>Sorex araneus</i>	Period (spring/autumn)	112	7.1	NA	24.5	< 0.001
		Snow cover in winter	111	3.3	- 0.84	11.4	< 0.001
	<i>Apodemus flavicollis</i>	Year	103	0.9	0.88	6.3	0.045
	<i>Myodes glareolus</i>	Year	101	2.1	0.92	10.7	0.001
	<i>Microtus agrestis</i>	Year	104	0.4	- 0.12	1.9	0.159
	<i>Sorex araneus</i>	Year	104	2.7	- 0.94	8.8	0.003

Rainfall in the previous summer negatively influenced abundances of both yellow-necked mouse in young spruce plantations and bank vole in mature beech forests (Fig. 5b). In young spruce plantations, snow cover had a negative impact on abundances of field vole and common shrew (Fig. 5d).

Spring and autumn abundances differed significantly only in yellow-necked mouse in mature beech forests and common shrew in young spruce plantations (Table 3). Whereas spring abundances of yellow-necked mouse were higher compared to autumn (Fig. 5e), the abundances of common shrews showed the opposite trend (Fig. 5f). Relative abundances of masts in the previous year had a positive effect on abundances of bank vole and yellow-necked mouse in both habitats and in both periods (Table 4, Fig. 6) with two exceptions; autumn abundances of yellow-necked mouse in mature beech forests showed an indicative relationship with masting and spring

abundances of yellow-necked mouse in young spruce plantations could not be analyzed due to insufficient data variability.

Discussion

Community structure in different habitats

The structure of the small mammal community differed greatly between the studied habitats, and we also found significant differences among localities. Higher species diversity, mainly composed of field vole, common shrew, bank vole, and yellow-necked mouse (93% of small mammals caught), prevailed in the young stands of blue spruce with dense hairy reed grass undergrowth at higher altitudes (800 m a.s.l.), while lower species diversity dominated by yellow-necked mouse and bank vole (96% of small mammals caught), was found in

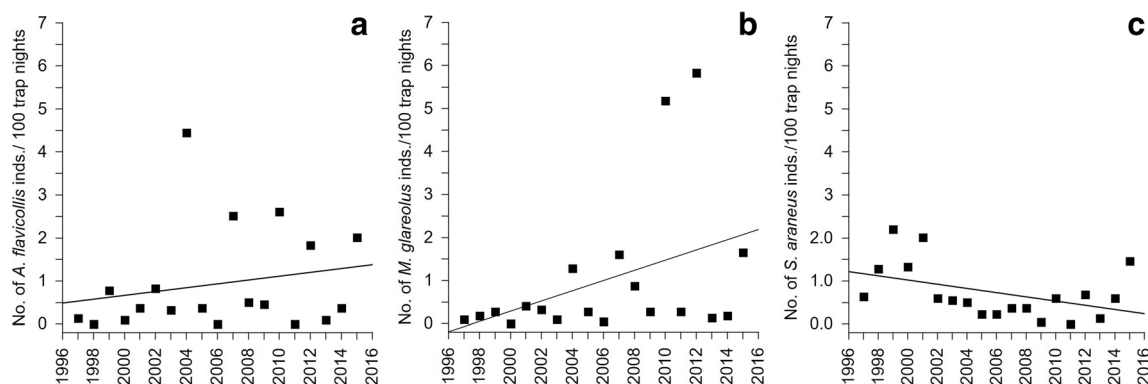


Fig. 3 Changes in abundances (spring and autumn together) of **a** *Apodemus flavicollis* ($p = 0.045$), **b** *Myodes glareolus* ($p = 0.001$), and **c** *Sorex araneus* ($p = 0.003$) during the period 1997–2015 in young spruce plantations. Abundances are expressed as the numbers of individuals per 100 trap nights

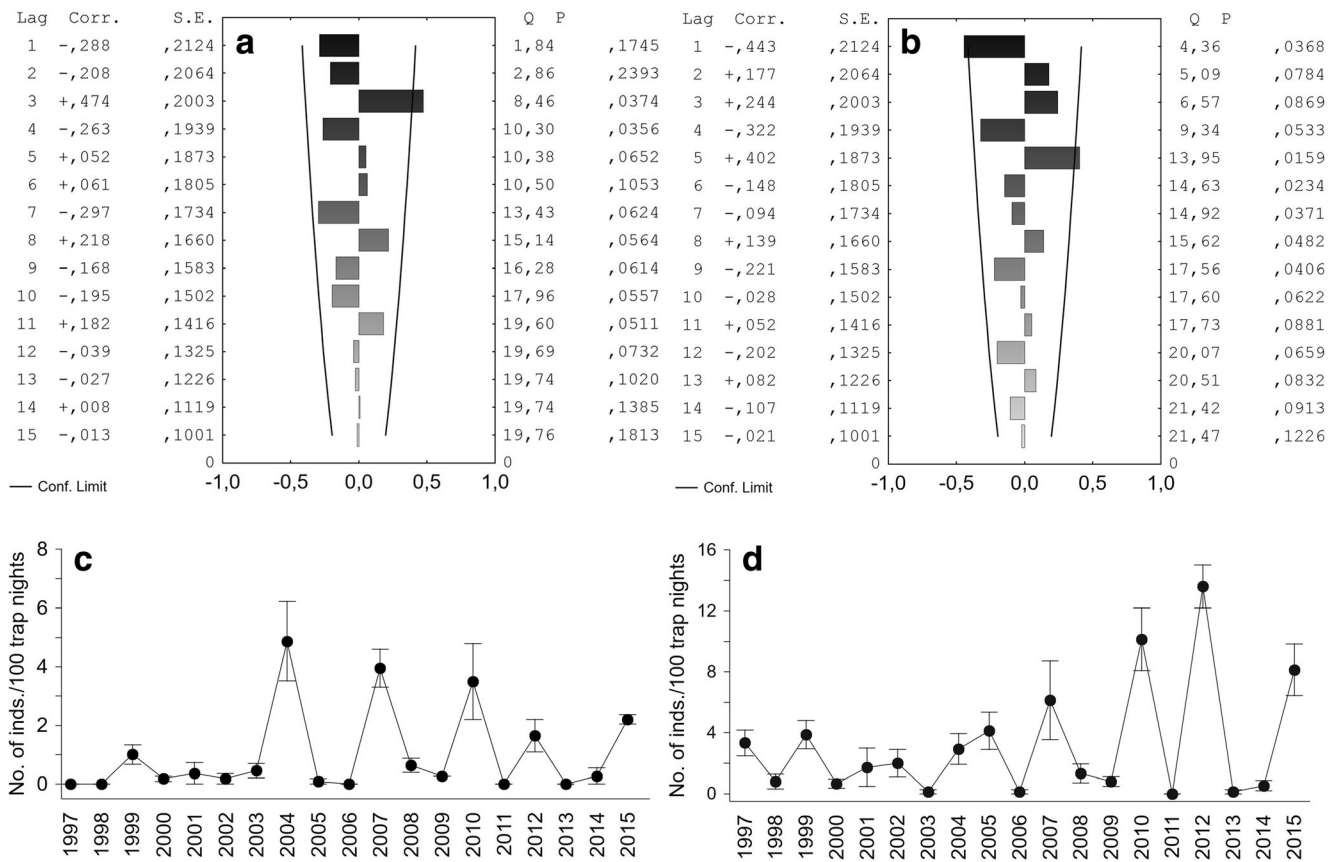


Fig. 4 Autocorrelation functions and yearly mean abundances (with SE) of *Apodemus flavicollis* in spring in young spruce plantations (a, c) and *Myodes glareolus* in autumn in mature beech forests (b, d) during the period 1997–2015

the mature European beech forests with sparse undergrowth vegetation at lower altitude (500 m a.s.l.). These findings are in agreement with our assumption and previous findings (Niethammer and Krapp 1978, 1982).

Long-term population trends

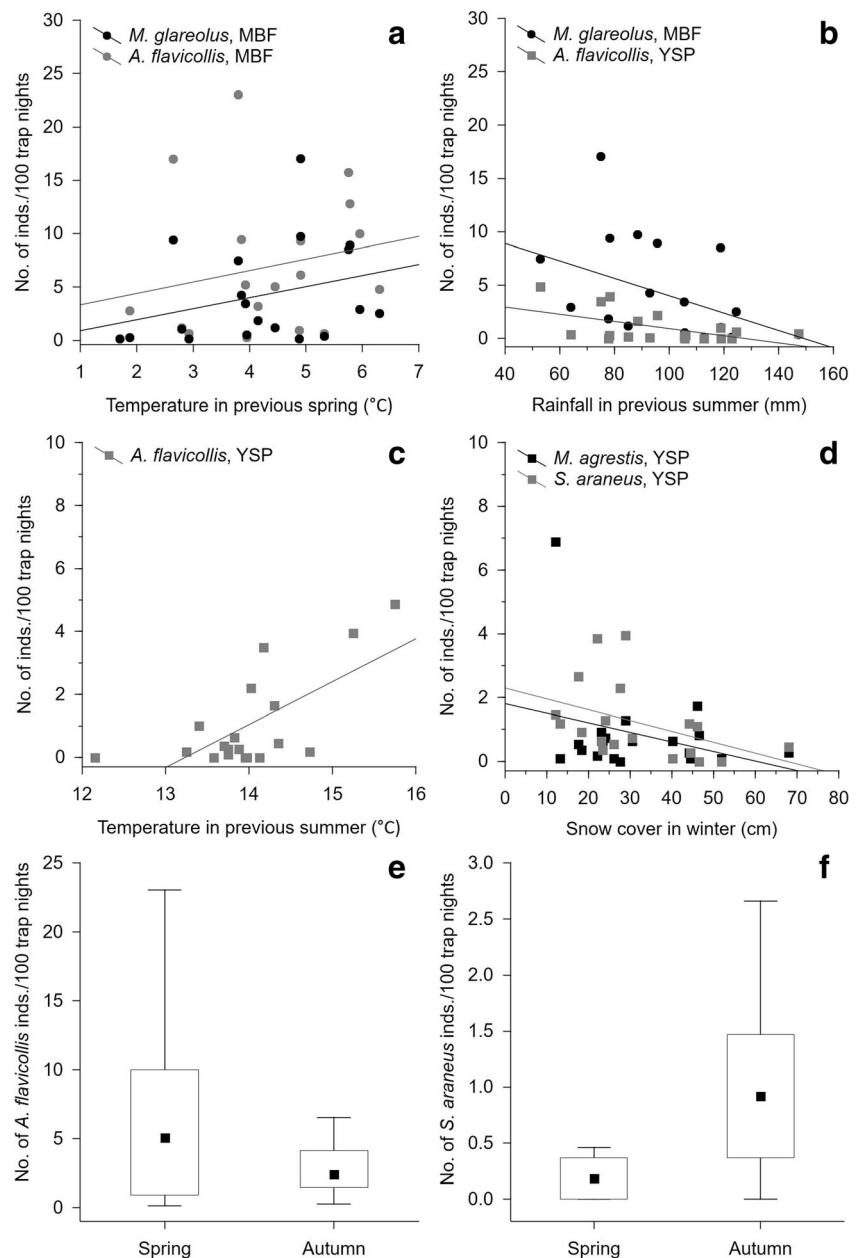
During the 20-year period (1997–2015), we found changes in small mammal communities only in young spruce plantations where bank vole and yellow-necked mouse became more dominant, while the abundance of common shrew decreased. These results are congruent with expected general trends in small mammal communities during the process of forest succession, i.e., species of open areas such as common shrew colonize early successional stages (unstable environment), while typical forest species such as bank vole and yellow-necked mouse inhabit more stable forest environments (Sundell et al. 2012). Moreover, in young spruce plantations, the abundance of bank vole increased substantially in the last 5-year period (2011–2015) during which a large proportion of the non-native blue spruce (more than 50% trees lower than 1 m) had been substituted with seedlings of Norway spruce. These findings probably result from the preferences of bank vole for Norway spruce seedlings, with their frequently

consumed apical buds, stems, bark, and young shoots (Gill 1992; Huitu et al. 2009; Lyly et al. 2014).

Population cycles

We did not record any cycles in field vole, but we found clear 3-year spring cycles in yellow-necked mouse in young spruce plantations. We also found 5-year autumn cycles, mixed with indicated 2- and 3-year cycles, in bank vole in mature beech forests. Both yellow-necked mouse and bank vole cycles in mature beech forests were positively affected by beech masting. In northern Europe, it was documented that pronounced vole population dynamics were often driven by predation from mammal and avian predators (Hanski et al. 2001; Korpimäki et al. 2002). However, such regulating mechanisms have not been confirmed for low-amplitude and irregular vole cycles in temperate zones (Korpimäki et al. 2005). In our study site, the dietary composition of the most abundant bird of prey population, i.e., boreal owl (*Aegolius funereus*), is related to the availability of yellow-necked mouse in young spruce plantations, but no relationship between predator-prey densities was found (Zárybnická et al. 2013). Instead, dynamics of granivorous species in the temperate zone are driven by masting events (e.g., Tattersall et al. 2002; Zwolak et al. 2016), as indicated also by our findings. Moreover,

Fig. 5 The relationships between **a** temperature in the previous spring (February–May) and abundances (spring and autumn together) of *Apodemus flavicollis* and *Myodes glareolus* in mature beech forests (MBF), **b** rainfall in the previous summer and abundances of *Apodemus flavicollis* in mature beech forests and *Myodes glareolus* in young spruce plantations, **c** temperature in the previous summer (June–September) and abundances of *Apodemus flavicollis* in young spruce plantations (YSP), **d** snow cover in winter (November–April) and abundances of *Microtus agrestis* and *Sorex araneus* in young spruce plantations during the period 1997–2015, and changes in spring and autumn abundances of **e** *Apodemus flavicollis* in mature beech forests and **f** *Sorex araneus* in young spruce plantations. Black box: median, white box: 25–75% of data, whiskers: non-outlier range. Abundances are expressed as the numbers of individuals per 100 trap nights



during the past few decades, vole population cycles have shown a pattern of dampened amplitude in Europe (Cornulier et al. 2013; Gouveia et al. 2015). However, our findings indicate that this trend may not be detected under local conditions.

Spring-autumn population dynamics

The relative abundance of field vole and common shrew was high in young spruce plantations only. In this habitat, abundances of both common shrew and field vole increased from spring (June) to autumn (October), but only common shrew abundances reached a significant peak in autumn compared to spring. In general, population densities of small mammals increase during the course of the vegetation season (Niethammer and Krapp 1978), but seasonal

and between-year fluctuations vary greatly, both temporally and spatially in temperate and northern areas (Korpimäki et al. 2005; Tkadlec and Stenseth 2001; Zub et al. 2012). Similarly to our findings, *Sorex* shrew and *Microtus* vole populations in western Finland have been found to usually peak in autumn (Korpimäki 1986). We have documented that the reproductive activity of both common shrew and field vole is prolonged to autumn in our study area (own unpublished data on reproductive activity of the species). Thus, we suggest the autumn peak of common shrew in our study area resulted from the seasonal pattern of reproduction (Niethammer and Krapp 1978).

Bank vole and yellow-necked mouse comprised substantial parts of small mammal communities in both studied habitats. In young spruce forests, abundances of both species did not

Table 4 The effect of the relative abundance of masts in the previous autumn on spring and autumn population abundances of yellow-necked mouse and bank vole in mature beech forests and young spruce plantations in the Ore Mountains ($n = 15$ years) (GLMM analyses)

Habitat	Dependent variable (No. of individuals/100 trap nights)	Period	<i>df</i>	% of explained variability	Beta	Chi	<i>p</i>
Mature beech forests	<i>Apodemus flavicollis</i>	Spring	14	5.4	0.75	5	0.0259
		Autumn	14	4.7	0.74	3.1	0.0805
	<i>Myodes glareolus</i>	Spring	14	32.3	0.15	29	< 0.0001
		Autumn	14	27.3	0.65	23.1	< 0.0001
Young spruce plantations	<i>Apodemus flavicollis</i>	Spring	14	0			1
		Autumn	14	19.8	0.62	8	0.0046
	<i>Myodes glareolus</i>	Spring	14	21.2	0.71	9.3	0.0022
		Autumn	14	14.3	0.72	10.1	0.0015

changed between the spring and autumn period, and spring and autumn abundances of bank vole and autumn abundances of yellow-necked mouse were positively correlated with the relative abundance of masts in the previous year. In mature beech forests, abundances of yellow-necked mouse peaked in spring and spring abundances were positively correlated with the relative abundance of masts in the previous year. Abundances of bank vole did not show any differences between spring and autumn, and both spring and autumn abundances were positively correlated with the relative abundance of masts. We suggest several non-mutually exclusive explanations for the variability in spring-autumn peaks across species and habitats:

1. Yellow-necked mouse starts breeding earlier (February-early March) than bank vole (late March) and reaches its population peaks in July; bank vole peaks when reproduction of yellow-necked mouse has usually finished (Bujalska and Grüm 2008; Bujalska et al. 2009, own unpublished data).
2. Mature beech forests in lower altitudes may serve as “a core habitat” for both granivorous species during food shortage and severe winters (e.g., Krojerová-Prokešová et al. 2016; Sundell et al. 2012), while young spruce plantations with dense reed grass cover can provide a suitable food habitat with high grass seed production during the summer and autumn migration (Sundell et al. 2012).
3. Bank vole and yellow-necked mouse are characterized by interspecific interactions (Grüm and Bujalska 2000; Zwolak et al. 2016); as a result, bank voles may occupy less suitable habitats (Sundell et al. 2012), and yellow-necked mouse can postpone the beginning of breeding (Bujalska and Grüm 2008) or may suffer from a decrease in survival, recruitment and body mass (Sozio and Mortelliti 2016).
4. Population dynamics, which are greatly controlled via predation by avian and mammalian predators (Korpimäki et al. 2002; Korpimäki et al. 2005), can be more strongly affected in young spruce plantations where larger populations of boreal owl occur compared to mature beech forests (Zárybnická et al. 2015c).

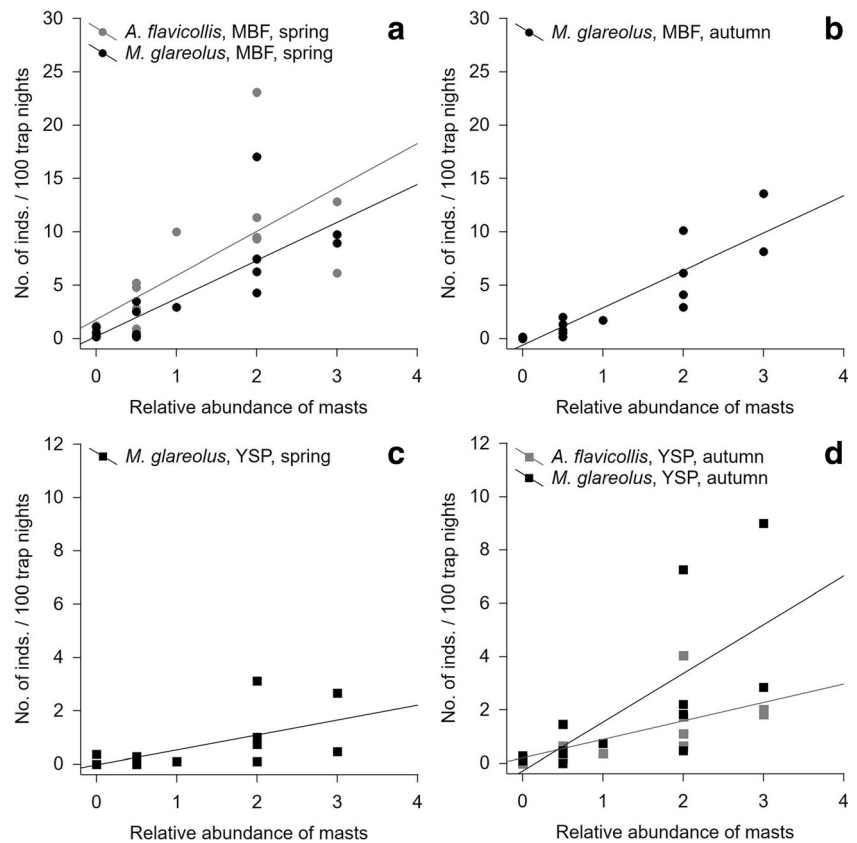
5. Young spruce plantations on the mountain plateaux are exposed to severe winter conditions and thus represent a less suitable habitat for overwintering than closed forests at lower altitude (Hille and Rodel 2014; Ylönen et al. 1991).

The effect of weather on population dynamics

In young spruce plantations, the densities of yellow-necked mouse were negatively correlated with rainfall and positively with temperature in the previous summer. In mature beech forests, abundances of yellow-necked mouse and bank vole were positively correlated with temperature in the previous spring, but effect of rainfall was only found in bank vole. Snow cover had no effect on densities of granivorous species. Several studies have shown that droughts and high summer temperatures are key factors affecting masting (e.g., Piovesan and Adams 2001), which is synchronous within temperate areas (Koenig and Knops 2005) and influences the abundance of granivorous species in the subsequent vegetation season (e.g., Pucek et al. 1993). In agreement with our findings, in neighboring German forests in Saxony, bank vole peaks occurred in the same years as bank vole and yellow-necked mouse peaks in our study area (2004, 2007, 2010, 2012), except for 2001 and 2005, and these peaks were related to beech masting in the previous year (Reil et al. 2015). Our findings support the contention that the dynamics of granivorous populations of small mammals in Central Europe are primarily driven by masting that are further connected with weather conditions, mainly rainfall.

Abundances of field vole and common shrew increased after winters with low snow cover (November–April), and this relationship was pronounced only in young spruce plantations on the mountain plateau. For ground-dwelling small mammals, snow cover has two important functions: insulation (e.g., Sipari 2015) and protection against predators (e.g., Bilodeau et al. 2013; Haapakoski and Ylonen 2013). However, unstable temperature conditions might lead to frequent ice formation on the ground that decreases availability

Fig. 6 Relationships between masting in the previous year (expressed as an index of the relative abundance of masts) and **a** spring abundances of *Apodemus flavicollis* and *Myodes glareolus* in mature beech forests (MBF), **b** autumn abundances of *Myodes glareolus* in mature beech forests, **c** spring abundances of *Myodes glareolus* in young spruce plantations (YSP), and **d** autumn abundances of *Apodemus flavicollis* and *Myodes glareolus* in young spruce plantations in the period 2001–2015 ($n = 15$ years)



of food resources (Korslund and Steen 2006). We suggest that warmer conditions and low depth of snow cover could shorten the time period when food resources are not available due to ice cover, leading to early onset of the vegetation season and increased vole densities.

Conclusions

While some issues like habitat preferences and dietary demands seem to be well understood, others, in particular the dynamics of small mammal communities and their driving forces, are still actively discussed (Krebs 2013). Here, we have documented the effect of habitat type, forest succession and management, food availability, weather, and interspecific competition on the dynamics of small mammal populations. Our results indicate that local biotic and abiotic factors play an important role for a particular species and should not be overlooked.

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Compliance with ethical standards The research was carried out in accordance with ethical standards following the Act No. 246/1992 Coll. on the protection of animals against cruelty, and it was approved by the

Ministry of the Environment of the Czech Republic (71735/ENV/16-3580/630/16).

Conflict of interest The authors declare that they have no conflicts of interest.

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