



Long-term monitoring of rodent and shrew communities in a biodiversity hot-spot in Austria using barn owl (*Tyto alba*) pellets

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ABSTRACT

Rodent and shrew populations are key components of many animal communities around the world. However, their population dynamics and the factors influencing their abundance are still not well understood. We analyzed rodent and shrew community composition and abundance at a UNESCO world heritage site, the Neusiedler See in Eastern Austria, using barn owl pellets. We identified temperature (mean and minimal monthly temperature) as well as maximum precipitation per day as significant drivers of the rodent and shrew presence. Our analyses showed that increased temperatures and dry summers will challenge most of the analyzed species and most likely lead to decreased abundances, which will also affect the already threatened Pannonic root vole (*Microtus oeconomus mehelyi*). Increased drainage efforts in this area would also lead to less ground water and dryer soil and therefore damage the local rodent and shrew populations. We show that barn owl pellets are a highly efficient way of monitoring rodent and shrew populations over a large area and enable researchers to decipher the factors influencing population and community dynamics. The use of pellet data, therefore, may still be one of the most efficient methods of assessing small mammal populations and their change over time.

1. Introduction

Rodent and shrew populations are an important component of many ecosystems around the world (Feldhamer, 2015). In the mammalian orders, rodents and shrews are the most diverse; for instance, rodents alone account for over 40% of mammalian species in the world (Barthelmess, 2016; Kay and Hoekstra, 2008; Wilson and Reeder, 2005). These small mammals are characterized by small home ranges, fluctuating population dynamics, high metabolic rates and populations vary from relatively stable to highly cyclic (Krebs, 2013). Rodent and shrew population dynamics are of central importance to the theoretical basis of population biology and regulation (Turchin, 2013). Following the r/K selection theory most rodents and shrews belong to the group of r-selected species (MacArthur and Wilson, 2001). They can reproduce several times per year, have high growth rates and produce many offspring; however, probability of surviving to adulthood is low. Given their high abundance at specific times of the year, they are an important part of the food chain for predators, as in our study, the barn owl (*Tyto alba*) (Goutner and Alivizatos, 2003; Paspali et al., 2013).

Understanding the mechanisms driving population decline and

growth has proven difficult (Batzli, 1992; Krebs, 2013). Depending on the species, rodents can show three to six year cycles of population peaks and crashes (Krebs, 1996; Norrdahl, 1995). The phenomenon of these cycles is still one of the greatest mystery in animal ecology. The amplitudes can be very large, population densities at the peaks can be up to 1000 times higher than at the lows of the cycle (Lomnicki, 1995). Little is known about the factors influencing these cycles, such factors could include: weather, population density, their overwintering success, food availability, dispersal and predator prevalence (Boonstra et al., 1998; Myers, 2018; Radchuk et al., 2016). We need to gain insights into the dynamics of multiple rodent populations in a given area over multiple years, in order to understand the interplay between species abundance and ecological factors (Milana et al., 2016; Previtali et al., 2009). To facilitate such monitoring, researchers have turned to assess species abundance and composition by using the undigested food parts that birds of prey regurgitate in pellets (Obuch et al., 2016; Paspali et al., 2013; Torre et al., 2015). Barn owls are opportunistic feeders; they feed on all small mammals they can subdue (Moysi et al., 2018; Taylor, 2003; Tores et al., 2005). Thus, the results from examining pellets can be used to assess species composition and abundance in an area. In addition,

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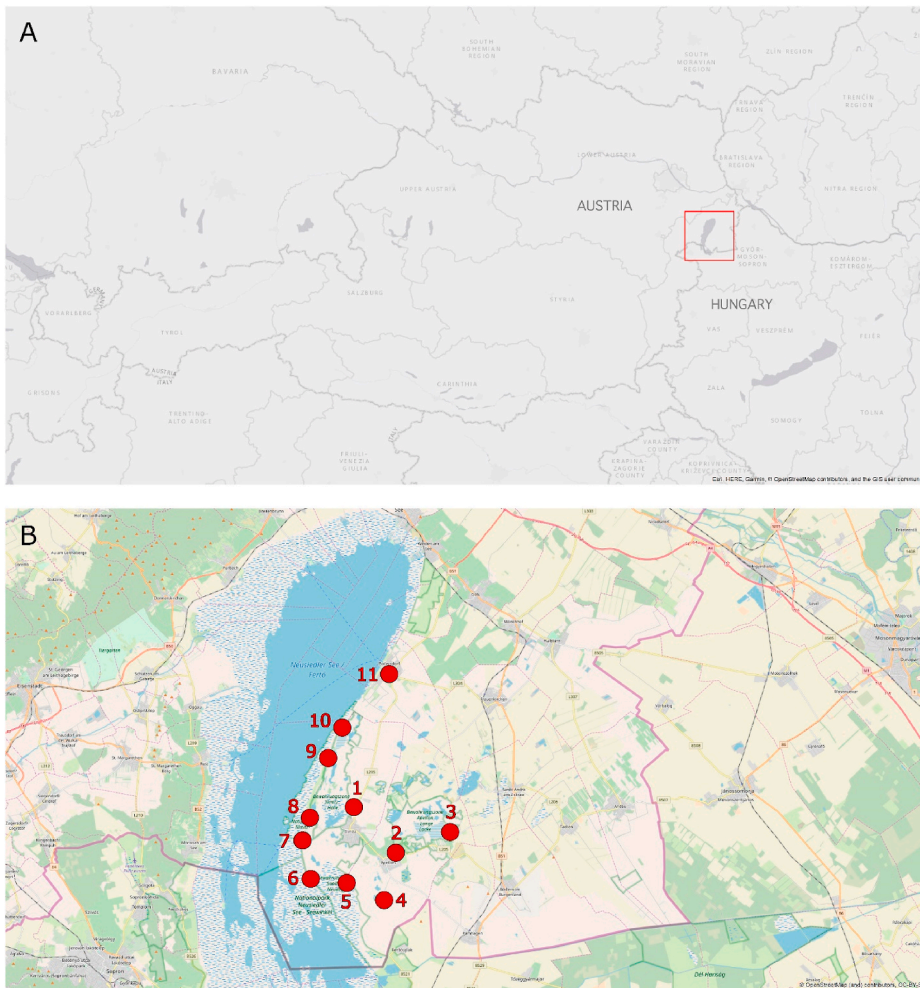


Fig. 1. Map (generated in ArcGis, 2018), showing the study area in Austria (A), as well as the detailed locations east of Neusiedler See (B). Water bodies are shown in blue, the border to Hungary is shown in violet. Red dots show the collecting points, named as followed: 1 Infozentrum Nationalpark Neusiedler See, 2 Rebschulgasse, 3 Seewinkelhof, 4 Apetloner Hof, 5 Graurinderstall, 6 Sandeck, 7 Warmblutkoppel, 8 Biologische Station Illmitz, 9 Przewalski-Ost, 10 Hölle, 11 Podersdorf. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pellets have been shown to be a more effective alternative for estimating a population compared to trapping (Andrade et al., 2016; Heisler et al., 2016; Torre et al., 2004).

In such pellets, beside rodents, another group of small mammals can be found frequently: shrews. They belong to the order of Soricomorpha and the family of Soricidae, in comparison to rodents they have an even higher metabolic demand. The population biology of shrews was subject of numerous studies (Churchfield et al., 1995; Wang and Grimm, 2007), however, despite the efforts, the factors driving their population dynamics are still poorly understood.

Barn owl pellets have been used successfully in several studies to decipher distribution and ecological preferences of rodents and shrews. For example, small mammal diversity seems to be higher in Tuscany compared to North-eastern Italy, which might be related to the extensive agriculture in the northeastern sampling region (Milana et al., 2016). In addition, pellet studies have been used to highlight decreasing small mammal diversity over the course of the last decades (Milana et al., 2018). Furthermore, it has been shown that pellets can also be used to analyze seasonal changes in populations, indicating, at least for southern Albania, that the ratio between rodents and insectivores remained stable across seasons (Paspali et al., 2013). Such data can facilitate identifying newly introduced species and update species distributions (Kiamos et al., 2019). For instance, pellet analysis revealed the unexpected absence of Savi's pine vole (*Microtus savii*) in southern Tuscany, an otherwise ubiquitous species in Italy (Battisti et al., 2019). In general, pellet data are valuable for evaluating differences in community composition and monitor species distributions and prevalence, i.e. to update red listed species (Heisler et al., 2016).

In the current study we use the pellets of the barn owl to gain insights into the rodent and shrew species composition and dynamics in the area east of Neusiedler See, we also investigated the effects of environmental parameters such as precipitation, temperature and season. We show that such parameters have an impact on rodent and shrew population cycles. Furthermore, we exemplify how rodent and shrew composition and dynamics can be monitored and used for faunistics by examining species remains in barn owl pellets.

2. Material and methods

2.1. The study area

Our study locations (Fig. 1) are all located east of the Neusiedler See (in the region Seewinkel), a lake in Austria, 47° 49' 4" N, 16° 44' 55" E, 115 m above the Adriatic. Extensive vineyards, meadows, agricultural land, emerging trees and periodic salt lakes dominate this region. The lake itself harbors a gigantic reed belt that builds up its own landscape (Fally, 2010). The combination of such diverse landscape offers an excellent habitat for mice, voles and shrews (Haberl and Krystufek, 2003; Hoi-Leitner, 1989). The natural and cultural assets of this region have also led to its acknowledgment as a world heritage site by the UNESCO in 2001 (Csaplovics, 2019).

2.2. Data collection

We analyzed pellets from barn owls collected between 2004 and 2016 (the total list of species is shown in Table S1). In sum we have 7871

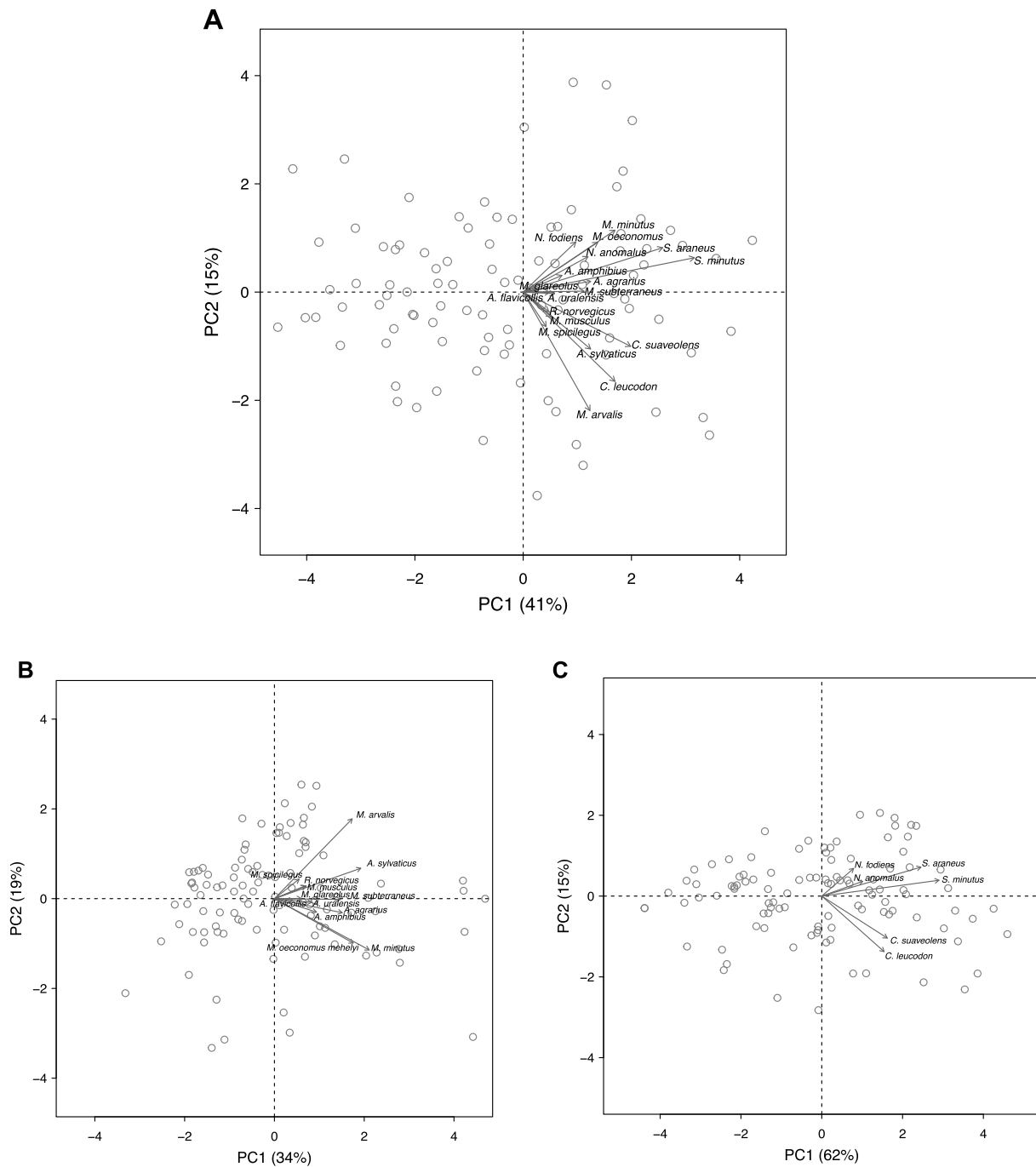


Fig. 2. Principal component analysis of Muroidea and Soricidae together (A), Muroidea (B) and Soricidae (C). Sampling events (pellets) are represented as open circles in this two-dimensional representation of the PCA results. The loadings of the individual species are plotted as arrows with the lengths scaled to the maximum PC values for each axis. The respective species names are given at the arrowheads.

individuals of the order Rodents, of the superfamily Muroidea (we pooled the two families Muridae and Cricetidae) and 8963 individuals of the order Soricomorpha, of the family Soricidae. For the nomenclature used in this paper, we followed the taxonomy presented by [Wilson and Reeder \(2005\)](#), however, using *Clethrionomys glareolus* instead of *Myodes glareolus*, as the scientific name for the red-backed vole, we are following the suggestion from a recent study ([Kryštufek et al., 2020](#)). Pellets found in one collection event are treated as one independent sample. One collection event may encompass multiple pellets, as the pellets from one collection event were always pooled. The number of small mammals found in one sample is assumed to be directly related to the abundance in the area.

The barn owl is a predator that regurgitates undigested parts of the food, like bones and fur, in pellets. The pellets are formed in the gizzard (muscular stomach) and allows all owls and predatory birds to remove indigestible material. In comparison to many other owls and birds of prey, the stomach pH-value is higher (less acidic) with the result that most bones of ingested prey are left undigested ([Smith and Richmond, 1972](#)). Therefore, intact skulls and mandibles are found in the pellets, even from small mammals such as the pigmy shrews (*Sorex minutus*) or the Eurasian harvest mouse (*Micromys minutus*) ([Andrews and Cook, 1990](#)). Once the skull or one mandible is available, in most cases the species can be identified. It has been well documented that the barn owl consumes all species according to their availability ([Berg and Ille, 2002](#);

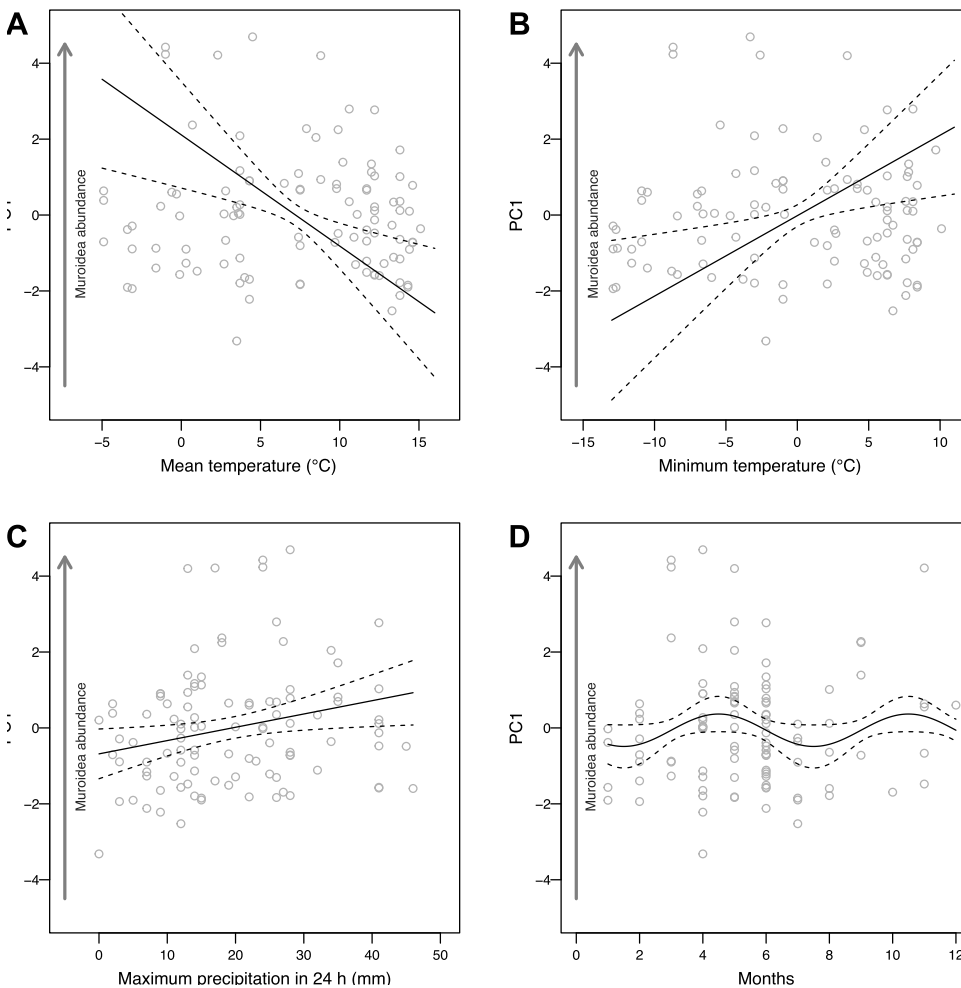


Fig. 3. The model fits for the Muroidea community (black line) with their 95% prediction interval (dashed lines) with PC1 as the dependent variable are shown for all components included in the final model after AIC-based model selection. This includes the mean temperature (A), minimum temperature (B), maximum precipitation in 24 h (C) and sine2 (D), which is here plotted in relation to the months in order to facilitate visual assessment of this variable. The underlying data are shown as open circles and the relationship between the PC1 values and abundance of Muroidea is shown using a grey arrow in each of the plots. See Table 1 for model details.

Tores et al., 2005; Moysi et al., 2018). Hence, sorting out pellets is a reliable method to gain information concerning small mammals in an area (Yom-Tov and Wool, 1997).

Owl pellets were sorted out and the content was determined by K. Stefke, using entire skull and mandibles or their remains for identification. The identification was done using a stereomicroscope and teeth and/or other morphological structures of the skull (Jenrich et al., 2012; März; Banz, 1987). Counting of individuals was done in the following manner: All calvariae and left and right mandibles were counted separately and the highest number, whether it was calvariae, left or right mandibles, was taken as the number of individuals. All collected remains from this study and the protocols are stored in the Mammal Collection of the Natural History Museum Vienna. We took the environmental data from ZAMG (Zentralanstalt Meteorologie und Geodynamik), the national meteorological and geophysical service of Austria. We took the measuring station in Andau, 47° 46' 21" N, 17° 2' 0" E, 118 m above the Adriatic. It is the nearest measuring station to our study area (approximately 8 km linear distance to the east from our collecting point number 3, Seewinkelhof).

2.3. Statistical analysis

The data was divided into two data sets for analysis. The first data set contained all individuals of the superfamily Muroidea (here we also pooled the two families Muridae and Cricetidae), excluding only *Rattus rattus* which was found only once in one sample. The second data set contained all individuals of shrews that were found. All statistical analyses were performed in R (R Development Core Team, 2012). In order

to increase reproducibility of our results and allow other researchers to employ the same methods with ease, the R script and data file including all performed analysis, the creation of tables and figures are published in the supplementary of this paper (see AnalysisScript-Pellets.R, CollectedSamples.csv and Environmental_Variables.csv). For all statistical analysis the abundance data was standardized using a log-transformation (using the formula: $\log(\text{data}+1)$).

To assess potential cycling through the year we calculated trigonometric terms, which describe specific cycling patterns (Pewsey et al., 2013) for trigonometric functions in linear models. We used the sine and cosine of months in radians for annual cycles (using the formula: $((2\pi)/12)\cdot\text{month}$). To assess biannual cycles as well we calculated the sine and cosine (later referred to as sine2 and cosine2) of the doubled radians of the month (reduced to modulo 2π) for biannual cycles (i.e. two abundance peaks per year).

In a first step we performed a principal component analysis (PCA) for each of the data sets using the function `princomp()`; this first analysis was also performed with both groups in one data set to show the relationship between Soricidae and Muroidea.

We then extracted the first principle component and used it in a generalized linear model assuming a Gaussian error distribution (using the function `glm()`) to model effects of year, sum of precipitation per month, maximum precipitation in 24 h, snow, maximum precipitation per day, minimum temperature (per month), mean temperature (per month), sine of the month, cosine of the month, sine2 of the month and cosine2 of the month. In order to avoid over fitting we employed the step AICc function to automatically perform backward AIC based model selection (Venables and Ripley, 2007). The best model was then used in the

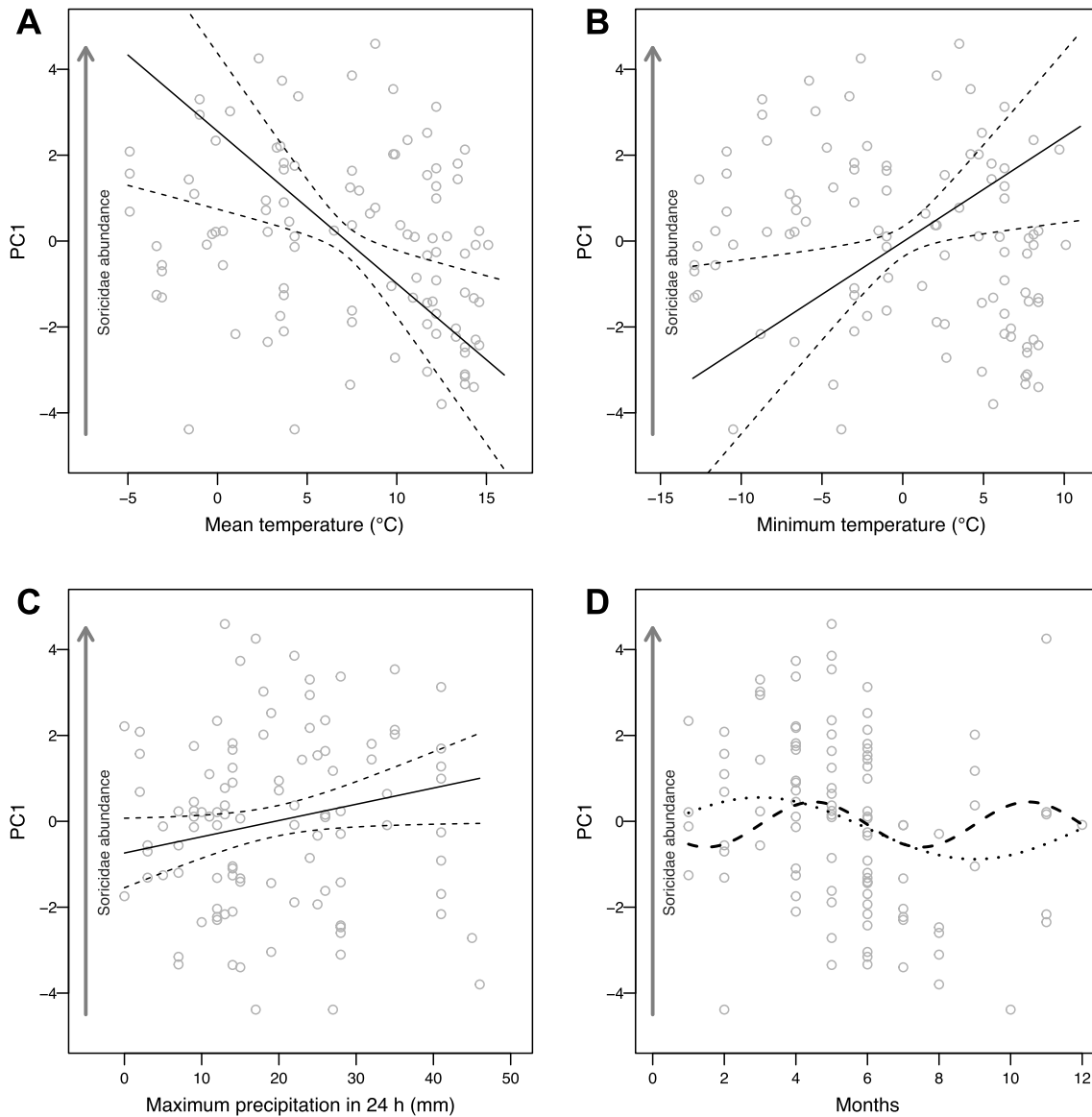


Fig. 4. The model fits for the Soricidae community (black line) with their 95% prediction interval (dashed lines) with PC1 as the dependent variable are shown for all significant components included in the final model after AIC-based model selection. This includes the mean temperature (A), minimum temperature (B) and maximum precipitation in 24 h (C). Two marginal significant components of the final model, sine2 dashed (black line) and sine (dotted line), are shown together in one graph plotted in relation to months (D), showing the cycling of the community in relation to each of those factors. The underlying data are shown as open circles and the relationship between the PC1 values and abundance of Soricidae is shown using a grey arrow in each of the plots. See [Table 2](#) for model details.

subsequent statistics and model fitting.

For all factors included in the chosen model we used the models further to plot model predictions (using `predict()`) including their 95% prediction intervals to visualize the effects observed in our data.

In order to show changes of abundance of all used species over the years we also plotted log-transformed abundance of each species over the years of this study. To identify species with significant abundance fluctuations between sampling years, we performed a non-parametric Kruskal-Wallis tests (using `kruskal.test()`) for each species, testing for differences between years.

3. Results

When all included species were analyzed in the same PCA, general trends were similar between Soricidae and Muroidea ([Fig. 2A](#)). We further split up the data in Soricidae and Muroidea in order to gain more detailed insights into the species co-occurrence in these two groups.

The PCA results for Muroidea showed a clear positive relationship of

all Muroidea species with PC1, which means that all later analyses with PC1 as the dependent variable indicated an increase of Muroidea abundance with increasing PC1 values. Most of the species clustered together around the zero line of PC2, however, *M. oeconomus mehelyi* and *M. minutus* were a bit separated from most other species and fell close together in the PCA space. Furthermore, *Microtus arvalis* showed a particular strong positive relationship to PC2 and therefore, appeared separated from the other species in the PCA space as well.

In the PCA for the sampled Soricidae, again, all species showed a positive relationship with PC1. Hence, the subsequent analysis can be interpreted in such way that increased values of PC1 mean increased abundance of Soricidae. Strikingly, in this family the members of the same genus were very close to each other in the PCA space, suggesting similar preferred ecological niches.

For both communities analyzed, abundance increased with decreasing mean temperatures. However, the positive relationship of abundance with minimum temperature, which might look counterintuitive at first, probably suggests a certain minimum threshold

Table 1

Generalized linear model showing main effects of mean temperature, minimum temperature, maximum precipitation in 24 h and sine2 on abundance of Muroidea (first principal component of Muroidea PCA).

Predictors	Muroidea (PC1)			
	Estimates	std. Error	Statistic	p
Max Prec. 24	0.04	0.02	2.27	0.025
Min T	0.21	0.08	2.61	0.011
Mean T	-0.29	0.10	-3.02	0.003
Sine2	-0.43	0.22	-1.95	0.054
Observations	103			

Table 2

Generalized linear model showing main effects of mean temperature, minimum temperature, maximum precipitation in 24 h, sine2 and sine on abundance of Soricidae (first principal component of Soricidae PCA).

Predictors	Soricidae (PC1)			
	Estimates	std. Error	Statistic	p
Max Prec. 24	0.04	0.02	1.98	0.050
Min T	0.24	0.10	2.42	0.017
Mean T	-0.35	0.13	-2.82	0.006
Sine	0.72	0.42	1.73	0.087
Sine2	-0.53	0.29	-1.81	0.074
Observations	103			

temperature required for increasing abundance (Fig. 3A and B, Fig. 4A and B, for model details see Tables 1 and 2). Muroidea and Soricidae abundance had a slightly positive relationship with the maximum precipitation in 24 h (Figs. 3 & 4C). Even when considering all available environmental data in our model selection approach, there was still a marginal significant cyclic pattern remaining which suggested a peak of Muroidea and Soricidae abundance in April/May and October/November (Figs. 3 & 4D). In addition, for Soricidae we observed a trending sine wave pattern, which would suggest more Soricidae animals in the first half of the year in comparison to the second half (Fig. 4D).

When we plotted the samplings for individual species over the years and tested for year differences, we observed significant changes between years for 10 out of 19 species, suggesting highly dynamic populations (Figs. 5–7). It is important to note, that abundance peaks and troughs are usually not restricted to a single species but seem to be similar for certain groups of species. For example, we observed an abundance increase in 2009 for most of the observed species and another one in 2013 (Figs. 5–7).

4. Discussion

We show highly fluctuating rodent and shrew population dynamics, which are correlated with abiotic factors such as temperature and precipitation. Furthermore, we demonstrate that barn owl pellets, a non-invasive and cost-effective sampling method, can be used to quantify

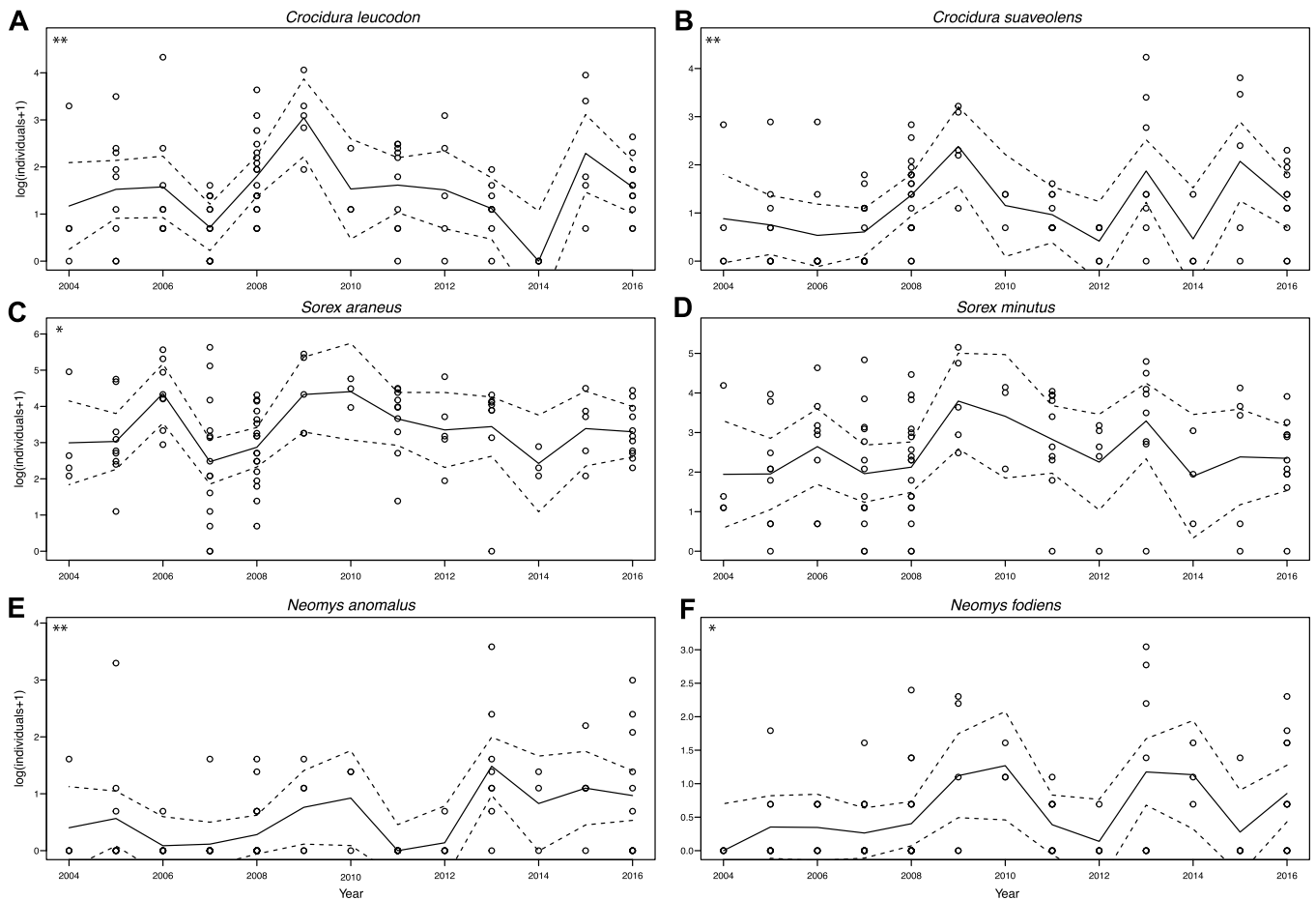


Fig. 5. Logarithmic counts of individuals for *Crocidura leucodon* (A), *Crocidura suaveolens* (B), *Sorex araneus* (C), *Sorex minutus* (D), *Neomys anomalus* (E), *Neomys fodiens* (F), for each year. Trendlines (black line) are shown together with 95% confidence intervals (dashed lines). Significant year differences according to the Kruskal-Wallis test are shown with asterisks (*: $p < 0.05$, **: $p < 0.01$), in the upper left corner in each panel.

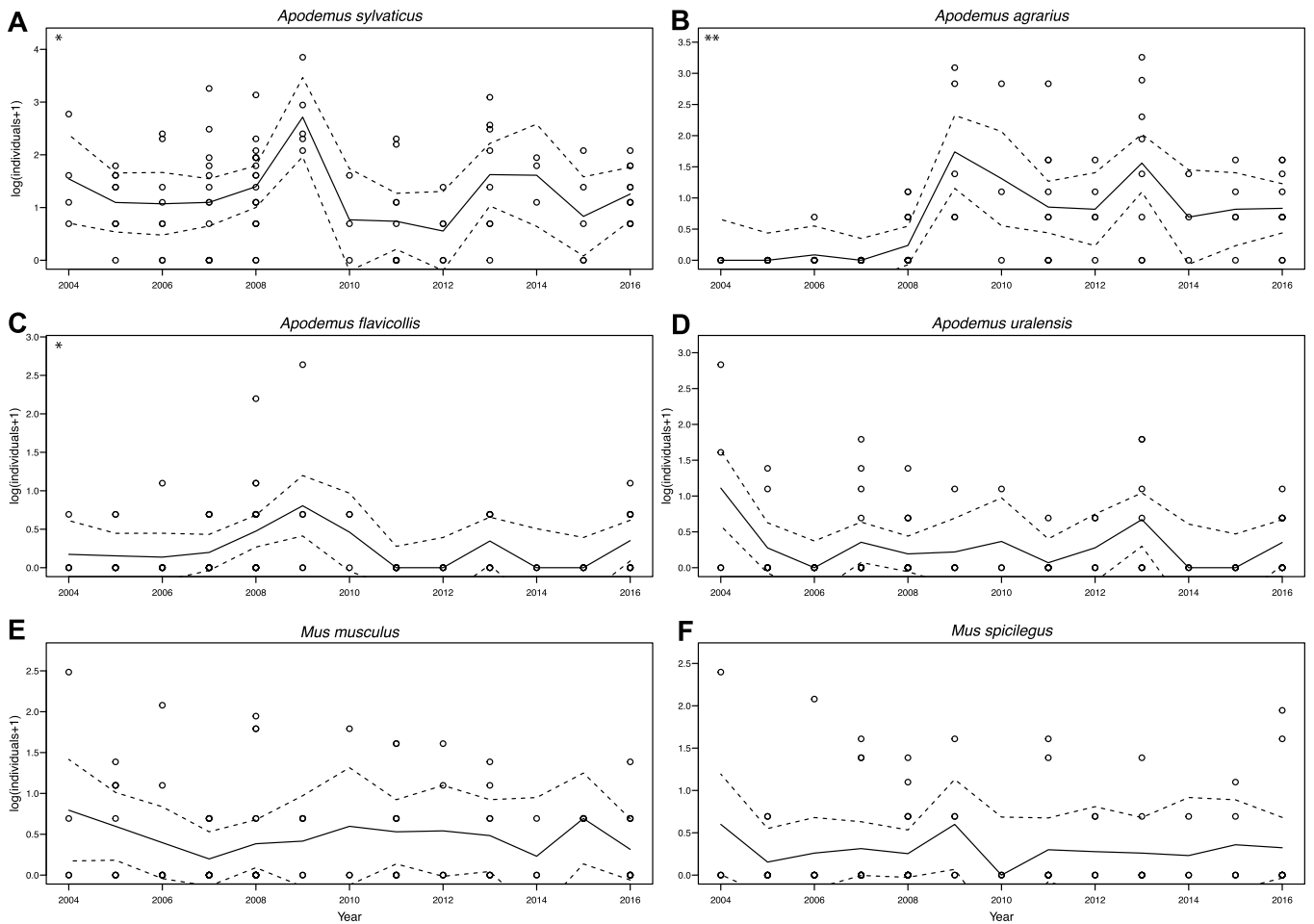


Fig. 6. Logarithmic counts of individuals for *Apodemus sylvaticus* (A), *Apodemus agrarius* (B), *Apodemus flavicollis* (C), *Apodemus uralensis* (D), *Mus musculus* (E) and *Mus spicilegus* (F) for each year. Trendlines (black line) are shown together with 95% confidence intervals (dashed lines). Significant year differences according to the Kruskal-Wallis test are shown with asterisks (*: $p < 0.05$, **: $p < 0.01$), in the upper left corner in each panel.

population dynamics; including monitoring threatened species and observing the arrival of new species in the area.

Although we have sampled and analyzed a wide array of rodent and shrew species, the general population trends appear to be similar, which is demonstrated by the positive correlation of abundance of all species with PC1. However, a closer look does reveal notable differences between taxa, with clustering of closely related species. For example, in the case of shrews the species split up in species clusters from the same genera; and *M. minutus* seems to show similarities to *M. oeconomus mehelyi*, separated from most other mice in the PCA space (see discussion below). As the barn owl pellets are essentially samples from a wide and undefined area around the sampling location, the co-occurrence of specimen in the same sample does not necessarily mean that the mice occur in the same microhabitat. This also means, if there is suitable habitat available for a specialist to avoid a more generalist species, both could show up as co-occurring in our analyses. However, our data does suggest general trends that influence rodent and shrew abundance. Taken together, rodent and shrews in our study appear to benefit from lower mean temperatures, if the minimum temperature does not drop too low (the cut-off appears to be around 0 °C), in addition, their abundance is positively affected by precipitation. Furthermore, the seasonal cyclic patterns show population increase in spring and fall, which result in two peaks. It would be interesting to monitor such seasonality in follow-up detailed studies, climatic changes could potentially shift the peaks towards an earlier start of the season, as well as causing a higher population to decrease in summer. Influence of climate change on

seasonality (time of births) has been shown, for example, in cattle and roe deer (Burthe et al., 2011; Plard et al., 2014). Our data exemplifies that one single factor alone is not sufficient to explain the observed dynamics, pointing towards the multiple-factor hypothesis for population dynamics (Krebs, 2013). While we cannot rule out the importance of intrinsic factors (e.g. stochastic population changes and multi-year cycles), similar trends across the different species, suggest that climate and weather are the main drivers of population dynamics. In addition, ‘year’ as a factor and most other non-environmental factors were not in the AIC-based selected model, suggesting again that environmental factors are the prevalent influences of population fluctuations. It is also important to add that the observed effects are unlikely due to changes in the barn owl predation or density. There were no density changes in the barn owl population reported in this well monitored area, therefore it is safe to assume that it remained stable over the period of our study.

Our data also revealed a newly established mouse species in the study area. In 1996, the first striped field mouse (*Apodemus agrarius*) was recorded for Austria in southern Styria (Spitzenberger, 1997). In 2003, the striped field mouse was first recorded at the Neusiedler See (Herzig-Straschil et al., 2004). In our data we had our first record of the striped field mouse in 2006 with one individual. Since then, it was present in the pellets every year with increasing numbers. Our data show that the striped field mouse has now established a population in the east of Neusiedler See and is a frequent member of the rodent fauna (Fig. 6D).

A species of interest in our study is the root vole, *M. oeconomus mehelyi*, which is a glacial relict in the area and of special conservation

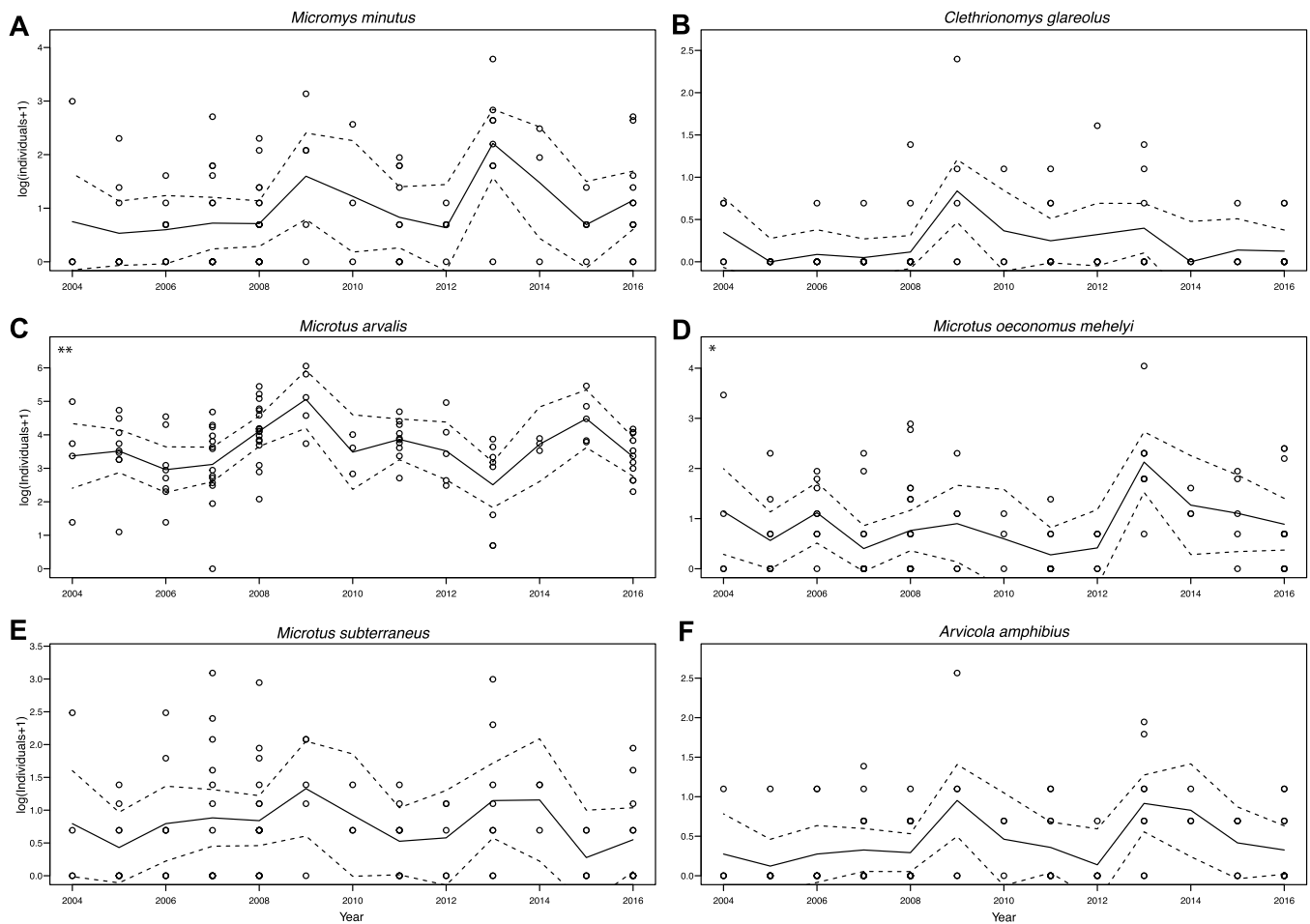


Fig. 7. Logarithmic counts of individuals for *Micromys minutus* (A), *Clethrionomys glareolus* (B), *Microtus arvalis* (C), *Microtus oeconomus mehelyi* (D), *Microtus subterraneus* (E), *Arvicola amphibius* (F) for each year. Trendlines (black line) are shown together with 95% confidence intervals. Significant year differences according to the Kruskal-Wallis test are shown with asterisks (*: $p < 0.05$, **: $p < 0.01$), in the upper left corner in each panel.

concern. It is a priority taxon of Annex II of the Habitats Directive and this subspecies is also listed on Annex IV of this directive. In consequence EU member states are obliged to inform the European Commission every six years about its conservation status (Thissen et al., 2015). In our study it clustered together with the harvest mouse (*M. minutus*), and in fact, they can be found in the same habitat, both species live in the reed stock of the Neusiedler See. The harvest mouse uses the stalks to build their nest, while the Pannonic root vole lives on the ground of the reed stock (Grimmberger et al., 2009), where the microclimate is colder than average. This indicates that our analyses can give insights into the co-occurrence on a medium scale, however, it is likely that species avoid competition amongst other things by habitat specialization, as it has been shown in several studies (Guélat et al., 2008; Morris, 1996). In comparison to other pellet studies which analyzed small mammal distribution based on ecological gradients (e.g. Milana et al., 2016; Milana et al., 2019), we focused on a smaller geographic area. Nevertheless, we show that pellets can also be used to decipher local climate influence and seasonal cyclic behavior of population dynamics.

Our data show that the majority of species analyzed can deal well with cooler climates. Increased precipitation and decreased temperature led to an increased abundance overall. For example, 2013 was marked with a cold and wet spring. The amount of the monthly sum of rainfall in March was 67 mm, while the average is only about one-half or one third of it. Also, in our sampling region, the temperature in spring dropped below the climatological average for this season. Nevertheless, many of the observed species, especially the cold adapted Pannonic root vole,

increased in abundance. Due to climate change, temperatures in Austria are expected to rise and the climate will become drier (Alexandrov et al., 2002). Temperatures will rise faster at the beginning of each year; therefore spring will tend to be shorter, hence also the vegetation has a shorter period to grow. Such drier climate will lead to sparser vegetation and, consequently, less food supply for rodents which will have an influence on the density of small mammals. Observed fluctuations in rodent density associated with rainfall triggers a large increase of food resources and hence populations become larger (Previtali et al., 2009). A continuous monitoring may be necessary to observe if the Pannonic root vole and other small mammals can handle the rising temperatures and dry summers. Population responses to local weather conditions can help understand the short-term impacts of climate change.

The agricultural land-use in the last decades has changed the available soil. In south Tuscany, anthropogenic disturbances simplifying the landscape matrix (mechanical agriculture and use of chemical products) induced an increase in mice and a decrease of shrews of higher trophic level (Battisti et al., 2020). For Salento (Italy) the level of human influence could also be considered as one of the causes of the low values of richness, diversity, and trophic levels of small mammals (Battisti et al., 1997). The common use of drainage systems in our study area further increases the pressure on the mammal communities by decreasing water in the soil and expansion of arid areas. Historically, this area was dominated by extensive wetlands and flood-plain, however, it is threatened by agricultural land use and a loss of connectivity between habitats, which are vital components of thriving small mammal communities (Bauer, 1960; Hoi-Leitner, 1989). The main threats to the root

vole and other rodents as well as shrews are habitat loss, fragmentation and degradation due to a changed water regime, the abandonment of traditional management of lowland meadows and reed beds. Consequently populations will suffer from genetic isolation (Thissen et al., 2015).

It will be up to the conservation management to preserve sufficient ground water and protect natural and semi-natural habitats to allow stable populations of small mammals. They are an important part of the studied ecological system not only, but also, as the most important food supply for birds of prey. The methodology used in the current study provides a first hint of the complex population dynamics of small mammals around the Neusiedler See, however, we show clear trends in response to abiotic factors (temperature and rain) which already inform conservation management and will help to estimate effects of land-use and climate changes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2020.103660>.

Author contributions

KS identified species, prepared and interpreted data and wrote the paper. LL analyzed and interpreted data and wrote the paper.

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