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Article

Numerical response of owls to dampening of the population cycles of the small mammals in Latvia

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Simple Summary: This article proves dampening of the small mammal population dynamics and describes the numerical response of owls in Latvia. Numerical response is measured in diet, breeding performance and population change trends in six owl species. Different species showed different responses ranging from increased food niche breadth in more plastic species to reduced breeding performance and decreasing population size in more specialized ones. Authors found evidence of dependency of eagle owl on voles via carry-over effect to reduced breeding performance. Species more specialized to breeding in mature forests showed stronger population declines, as mature forests are important for owl breeding as well as hold higher vole densities. In conclusion, owl response to depleted populations of small mammals was quantified and it was suggested as an important covariate to overwhelming impacts of forestry.

Abstract: Strong numerical and functional response of owls to voles in cyclic environments is well known, but there is insufficient knowledge from boreonemoral region, in particular, with depleted populations of the small mammals. In this study we describe the dynamics of the small mammal population in Latvia from 1991 to 2016 and link them to owl population characteristics. We used food niche breadth, number of fledglings and population trends to describe the numerical response of six owl species to dampened small mammal population cycles. We found temporarily increasing food niche breadth in tawny and Ural owls. There were no other responses in tawny owl, whereas the breeding performance of three forest specialist species – pygmy, Tengmalm`s and Ural owls – were similar to vole crash years in Fennoscandia. Moreover, the populations of forest specialist owls are decreasing and the change in Ural owl can be attributed to the depletion of small mammal populations. We found evidence of carry-over effect in eagle owl arising from strong correlation of declining breeding performance with the small mammal abundance indices in previous autumn. We conclude that dampening of the small mammal population cycles is an important covariate to overwhelming impacts of habitat destruction with stronger response in more specialized (to prey or habitat) species.

Keywords: diet; breeding performance; population trends; Aegolius funereus; Asio otus; Strix aluco; Strix uralensis; Bubo bubo

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1. Introduction

Small mammals play an important role in ecosystem functioning and various ecological processes. This role ranges from influence on a natural succession [1], through influence on plant and microorganism community composition and chemistry [2] to demographic processes of small mammal predators [3-6] and even population processes and behavior of directly unrelated species [7-9]. The effects of small mammals on demography of birds of prey are so strong that the analysis of the breeding performance of the latter can reveal large scale spatial-temporal patterns of population dynamics of the former [10]. In the boreal region small mammal populations typically show strict cyclicity over long time periods and hundreds of kilometers [10-12]. On a smaller spatial -scale synchrony of cycles is documented also in western Europe [13] and the boreonemoral region – Baltic states [14-16]. Based on long-term rodent abundance studies in Fennoscandia [12], substantial support for the predation hypothesis being the main reason for small mammal population cyclicity is gathered [17]. This hypothesis suggests that the rodent abundance gradient reflects the relative influence of destabilizing specialists and stabilizing generalists on vole dynamics, modulated by the presence of the snow cover [17]. This hypothesis is also supported by the characteristics of rodent dynamics in central and western Europe [13]. In late 20th century rodent cycles showed irregularities and dampening, particularly in more northern latitudes [18-22]. Due to the large spatial extent, this dampening was explained by climate forcing – a decrease in delayed density dependence caused by milder winter conditions [23-25]. Yet, the generality of this hypothesis was refuted due to the return of the vole cycle in southern Finland [26].

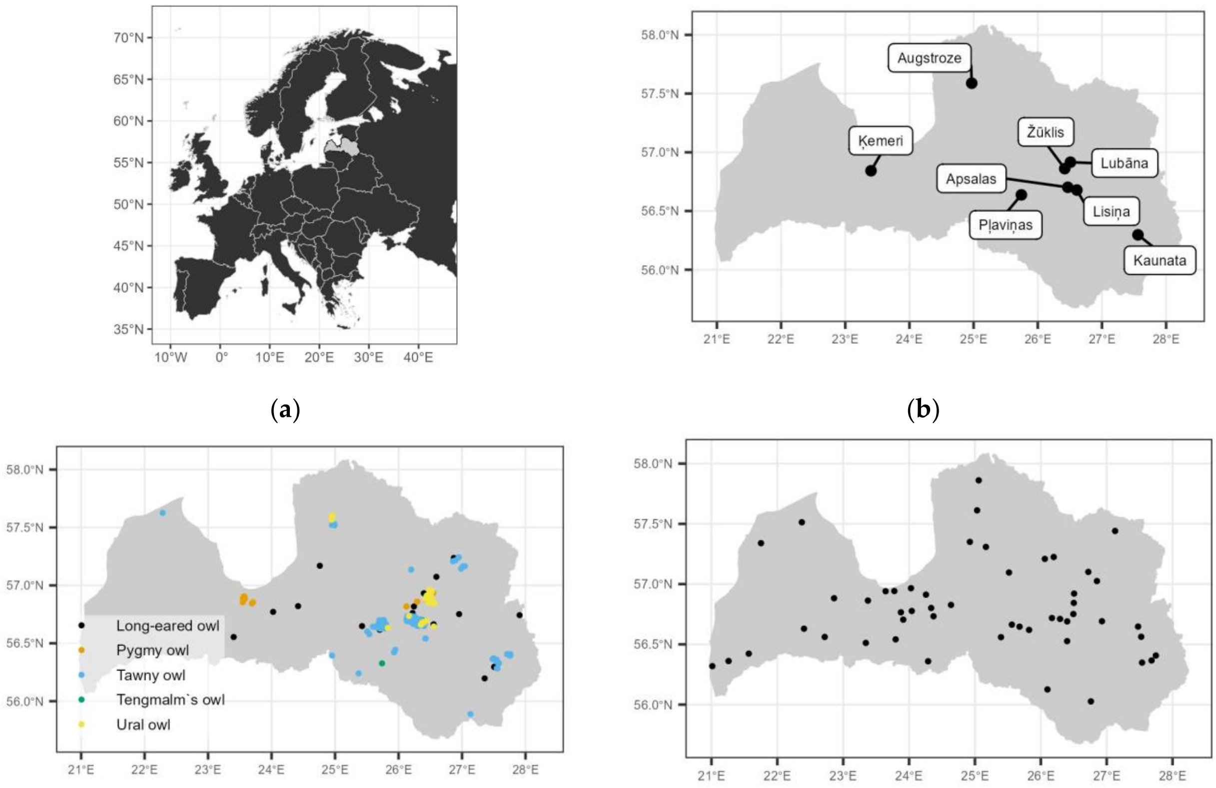
There is a substantial amount of evidence for the importance of small mammals, particularly voles, to owls. Firstly, voles form an important part of the owl diet ranging from more vole specialized long-eared owl *Asio otus* (hereinafter, ASIOTU) [27-31] and Tengmalm`s owl *Aegolius funereus* (AEGFUN) [32], to more generalist species like Eurasian pygmy owl *Glaucidium passernium* (GLAPAS) [33-34], Ural owl *Strix uralensis* (STRURA) [34-35], tawny owl *Strix aluco* (STRALU) [28, 34, 36] and eagle owl *Bubo bubo* (BUBBUB) [37]. Secondly, they are one of the key elements ensuring higher breeding performance (generally, [6, 34]; ASIOTU [29]; AEGFUN [38, 39]; GLAPAS [40]; STRURA [41]; STRALU [36]) and survival (ASIOTU [42]; AEGFUN [43]; GLAPAS [44]; STRURA [3, 39]; STRALU [36, 45]). Finally, vole density is known to affect the owl behavior ([46] and [47]), migratory decisions [32] and life history via the carry-over effect [48]. Most of the studies on the subject are performed in cyclic environments of Fennoscandia and there are very few from the Baltic states (but see ([28] and [36]) and references therein). We are not aware of studies focusing on boreonemoral region during prolonged periods of depleted small mammal population dynamics.

In this study, we describe small mammal population densities in Latvia 1991-2016 and link them to several population characteristics of six owl species long-eared owl, Tengmalm`s owl, pygmy owl, Ural owl, tawny owl and eagle owl. First, we describe the owl diet and its change to establish the importance of small mammals and, in particular, voles for different owl species and to divide owl species based on food niche breadth and the overall proportion of voles in their diet. Then we compare nationwide owl population trends and their slopes with cyclic vole populations and since dampening. And finally, we describe owl breeding performance and relate some demographic parameters to the observed population change.

2. Materials and Methods

2.1. Location and field methods

The study was performed in Latvia, Northern Europe (Figure 1 (a)). The country is located in the boreonemoral region [49] with a humid continental climate [50]. It lies within the continuous distribution range of all six owl species (ASIOTU, AEGFUN, GLAPAS, STRURA, STRALU, BUBBUB) investigated [51].



(**a**) (**b**)

(**c**) (**d**)

Figure 1. Study site locations: (**a**) Latvia in Europe; (**b**) the small mammal monitoring areas; (**c**) owl diet sampling sites; (**d**) owl population change monitoring areas.

2.1.1. The small mammal monitoring

The monitoring for the relative abundance of the small mammals was performed with snap-traps from 1991 to 2016. It consisted of two schemes: occurring in two transects per site with one in forest and one in meadow (1), and with 11 transects per site: one in meadow and 10 in different forest habitats (2).

The first scheme was officially run from 1991 to 2011. 100 snap-traps per transect (approx. 5 m between traps) were used in autumn (August-September) for three to four days [52]. Volunteers partially repeated this monitoring in 2015-2016. Altogether this scheme was conducted in four sites (Figure 1 (b)), but not every site was monitored every year (Table 1).

The second scheme was performed in autumn (August-September) 2012-2016 by volunteers. In this scheme, 20-25 snap-trap transects (approx. 5 m between traps) were located in four areas (Fig. 1.b), though not all the areas were monitored every year. Forest transects were stratified into 10 categories representing soil fertility (two groups), drainage (drained vs. non-drained) and stand age (<7 years, <80% of the rotation age, >=80% of the rotation age; minimum rotation ages for dominant tree species in Latvia are stored in Table A1), based on State Forest Registry (stand level inventories), as follows:

- YP – young (clearcuts and stands <7 years old) stands on poor soils;
- YF – young (clearcuts and stands <7 years old) stands on fertile soils;
- MPU – medium-aged (between 8 years and 80% of rotation age) stands on poor soils without drainage;
- MFU – medium-aged (between 8 years and 80% of rotation age) stands on fertile soils without drainage;
- MPD – medium-aged (between 8 years and 80% of rotation age) stands on poor drained soils;
- MFD – medium-aged (between 8 years and 80% of rotation age) stands on fertile drained soils;
- OPU – older (>=80% of the rotation age) stands on poor soils without drainage;

- OFU – older (>=80% of the rotation age) stands on fertile soils without drainage;
- OPD – older (>=80% of the rotation age) stands on poor drained soils;
- OFD – older (>=80% of the rotation age) stands on fertile drained soils.

Table 1. The description of the small mammal monitoring effort

Sample Area	Period	Description
Apsalas	1991-2011; 2015-2016	Two habitats: meadow and forest (OFD); 100 traps per transect
Lisiņa	2001-2005	Two habitats: meadow and forest (OFU); 100 traps per transect
Žūklis	2003-2011; 2015-2016	Two habitats: meadow and forest (OFD); 100 traps per transect
Ķemeri	2006-2010; 2015-2016	Two habitats: meadow and forest (OFU); 100 traps per transect
Kaunata	2012-2016	11 habitats: meadow and 10 forest classes; 20-25 traps per transect
Lubāna	2012-2016	11 habitats: meadow and 10 forest classes; 20-25 traps per transect
Pļaviņas	2012, 2016	11 habitats: meadow and 10 forest classes; 20-25 traps per transect
Augstroze	2012-2016	11 habitats: meadow and 10 forest classes; 20-25 traps per transect

2.1.2. Owl diet during the breeding season

Owl diet analysis was based on prey remains and pellets found in nests or on the ground near the nest. Only material from a single breeding occasion was used, based on annual nest-box and cavity inspections (GLAPAS, AEGFUN, STRALU, STRURA) or an assumption that pellets cannot survive for many months in open nests or on the ground in the case of ASIOTU. The material was collected in autumn or winter from nest-boxes and cavities and during chick ringing from ASIOTU nests. When collecting material, all the soft contents of nest-boxes and cavities were removed. In the case of ASIOTU, all the useable material was collected. The distribution of the owl diet sampling sites in Latvia is shown in Figure 1 (c).

Analysis of the remains of prey and the identification of the minimal number of individuals was performed as described in Vrezec et al. [35]. Insects were assumed to represent 1g biomass and amphibians-and-reptiles to weigh 16 g – average body mass of 100 measured individuals during chick ringing in 2016. In birds, reference size group (i.e., woodpigeon, song thrush, chaffinch, chiffchaff) weight from general literature [53] was used. Region-specific weight of mammals from our trapping data or literature [28, 54] was used. We assumed young hare *Lepus sp.* to weigh 350 grams.

2.1.3. Owl population change monitoring

The monitoring for owl population change was performed with traditional (territory mapping with playback broadcasting) methods [55–59] in permanent sample areas 1991-2020 as well as with fully standardized point-counts (with playback broadcasting) from national Breeding Birds of Prey Monitoring [60] in 2015-2022. The spatial distribution of monitoring sites is shown in Figure 1 (d).

2.1.4. Owl breeding performance

As a nest level descriptor of the breeding performance strongly related to food availability, we used the number of fledglings per successful nest. We used four data sources: nest-box inspections (1), information reported by ringers to Latvian Ringing Centre (2); reports in the Breeding Birds of Prey Monitoring and the previous Monitoring for Owls (3), and citizen scientist reports in nature observation platform dabasdati.lv (4). The first two and partially also the third source cover information from the nests during ringing just before the young fledge. The citizen science and partially monitoring databases cover information on the number of young soon after fledging.

Most of the information before 2010 (apart from monitoring data) did not contain exact coordinates to be used in spatial filtering and removal of duplicate records. Therefore, we joined nest-box inspection, monitoring and ringing databases, based on location attributes (indicated by nest name given by the ringer – most often also the person performing monitoring) to remove duplicates. We used citizen science reports only if there was no other information on the species in the particular year in the particular spatial reference. As a spatial reference, we used the national 1 km projected coordinate grid (epsg: 3059), if coordinates were known or the reported municipality otherwise.

2.2. Data analysis

We used software R [61] in data analysis, with package 'tidyverse' [62] for data processing and visualizations and 'sf' [63] for spatial data. We treated results with p-values≤0.05 as statistically significant but also reported insignificant results with full test description.

2.2.1. Small mammal monitoring

We standardized the small mammal trapping data to the number of individuals per 100 trap-days for further analysis and filtered only for autumn counts due to low representation of spring data. We used a graphical representation of the standardized counts per sampling area and habitat to compare variability between sites and habitats. We used generalized linear mixed effects modelling (GLMM) to compare the differences in standardized densities between sampling areas, age classes and soil fertility classes (including meadow habitats as a separate class in the latter two). We created two main effects models per comparison:

- random intercept per transect and the comparable variable in the fixed part;
- random intercept per transect, the comparable variable and year as a factor in the fixed part.

We used the Poisson family with a logarithmic link function and selected the best model based on the lowest value of sample size corrected Akaike information criterion value (AICc) [64]. We used marginal means contrasting with Tukey`s p-value correction for a *post-hoc* analysis between groups of the comparable variable. For mixed effects modelling we used R package 'lme4' [65], and package 'emmeans' [66] for contrasting.

We found no differences in peaks nor depressions between the sample areas in graphical analysis or mixed effects models, therefore, we used information from all the areas to obtain country wide small mammal population change index with TRIM analysis implemented in R package 'rtrim' [67]. The baseline model in this tool can generally be written as:

$$\ln(\mu_{ij})=\alpha_i+\beta_j, \tag{1}$$

where μ_{ij} is an expected count, α_i is a site parameter for the site i and β_j is a time point parameter for year j (for full explanation see [68]). We created a model (model=3) for the number of individuals pooled over species (the small mammals) and separately for voles of genus *Microtus* and *Clethrionomys*. We evaluated serial correlation and overdispersion, and selected the best model based on the lowest AIC value. We used the multiplicative slope of imputed values reported by TRIM to describe the overall population trend.

We used graphical evaluation and Pearson`s correlation analysis to compare the dynamics of both vole groups using yearly indices produced by TRIM analysis. We evaluated the presence of cyclicity with autocorrelation function analysis.

2.2.2. Owl diet during the breeding season

We used only the samples with at least 5 mammal prey individuals to avoid the influence of some very small samples. We used the small mammal data grouped to genus, as used in [69], and other prey groups as described in section ‘2.1.2. Owl breeding season diet’ to calculate Levin`s niche breadth (FNB):

$$B=1/\sum p_i^2, \tag{2}$$

where p_i is a fraction of a given prey in the total consumed biomass [70].

In supplementary material Table S1, we provide a description of the abundance and weight of the annual diet per owl species. For the description, we used the total number and cumulative biomass of the prey group, their arithmetical mean values, and proportions with Wilson`s 95% confidence intervals.

We used linear regression (LM) analysis to evaluate the overall temporal change in food niche breadth. In species with repeated samples from the same nest sites, we also created linear mixed effects models (LMMs) with nest ID as a random intercept. In the case of singularity in the random part, we used the result of LM [71-72], as there were too few replicates per nest to contribute to the model fit. Model coefficients in fixed part did not differ in these models. We fitted simple regression models with niche breadth as a response and year as a regressor variable. Both types of models were parameterized for Gaussian residual distribution with the identity link function.

Then we evaluated the effect of each small mammal population index previously described on niche breadth with the same LM and LMM approach. We fitted models with the independent variable of the year of breeding, admitting a possibly reduced effect as the small mammal yearly indices represent late summer to early autumn rather than late spring to early summer, when owl breeding occurs.

Additionally, we used the biomass proportion of bank voles and voles of genus *Microtus*, for regression analysis with estimated population indices and bank vole proportion with the index of *Microtus* voles. In this set of analyses, we used GLMMs with a random intercept for nest ID and generalized linear models (GLMs) if the identifier, due to the number of replicates being too low, did not contribute to model performance [71-72]. We used binomial family with logistic link function to compare the proportion of prey in the diet with its annual population index value in nature the same year.

Due to the small number of samples, we only described AEGFUN diet without further analysis.

2.2.3. Owl population change monitoring

Owl population monitoring started in 1990, but not all species had reliable information since the beginning. Due to its preference for large forest massifs, STRURA was covered only since 1993. Due to a lack of knowledge on monitoring GLAPAS, its population change can be analyzed only since 2004. Due to the low population size, we did not have reliable data on the population change of BUBBUB.

We combined data from both owl monitoring schemes, if sites had all the planned census activities – for sample areas, sufficient coverage marked by observer and for point count sites, four standardized visits in each point every year. To analyze population change, we used TRIM as described in section “2.2.1. Small mammal monitoring”. We used only sites with information from at least two years and comparable effort, according to prerequisites [73].

We calculated yearly indices and overall population change, described by multiplicative slope with standard error [68, 74], covering the whole available data period for species. Then we calculated two different slopes – with relatively cyclic small mammal population dynamics and since cycles had vanished. As a threshold for this division, we used 2004 which is:

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- approximate time since when the small mammal populations did not recover to previous peaks;
- approximate midpoint of small mammal monitoring;
- approximate midpoint of STRURA monitoring;
- beginning of GLAPAS monitoring.

To calculate before and after trends, we selected the necessary parts of yearly indices and performed linear regression on ln-transformed indices. We defined indices 2004-2016 as "after" and 1991-2004 as "before". To obtain significance tests, we transformed time to start with year 1 in each group to use in regression with interaction between time and period. We defined "before" as a reference level.

2.2.4. Owl breeding performance

As in most cases we were not able to match different breeding performance reports to an exact breeding location (nest or territory), we calculated annual mean values of spatially cleaned results. To provide more generalizable information, we calculated bootstrapped 95% confidence intervals from 1000 bootstrap resamples and used them in visualization. We used annual mean values to establish a temporal trend of overall change in breeding performance. As the amount of information varies among different owl species, we used slightly different approaches in further processing.

For two species (STRALU and STRURA) with most data available on a nearly annual basis over time, we compared temporal trends before and after the dampening of small mammal cycles in 2004. We used Gaussian linear regression with the annual mean number of fledglings as a response and compared trends between the periods as in population change analysis.

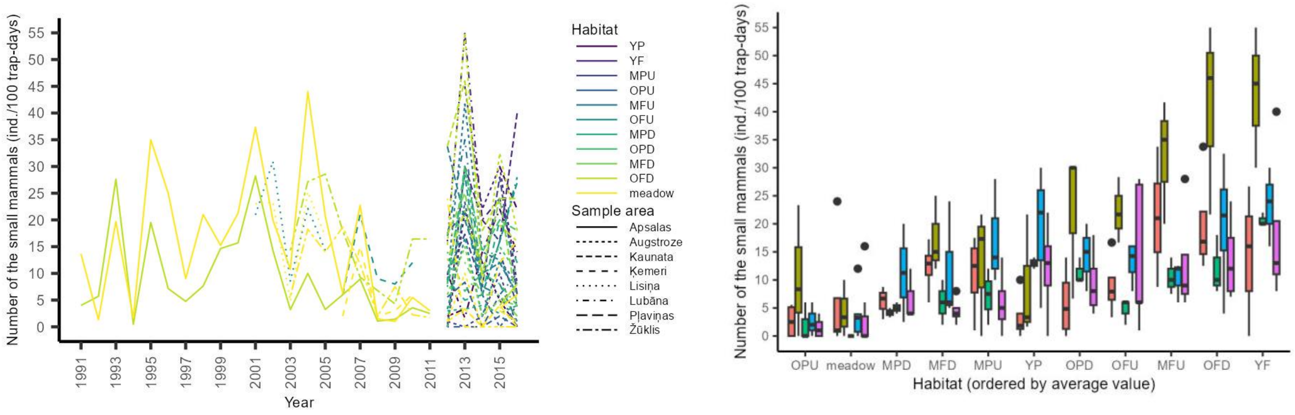
We used all the years available to correlate the annual mean breeding performance of STRALU and STRURA with small mammal population indices in the year of breeding and one year before to evaluate a possible carry-over effect. In the case of ASIOTU and BUBBUB we used a reduced timeframe to avoid possible artefacts due to irregular sampling and small sample size – from 2002 and 2001 respectively. We used Spearman`s rank correlation analysis due to some outliers and slightly curved scatterplot.

We used the R package 'Hmisc' [75] for bootstrapping and base R for correlation and regression analysis.

3. Results

3.1. Small mammal monitoring

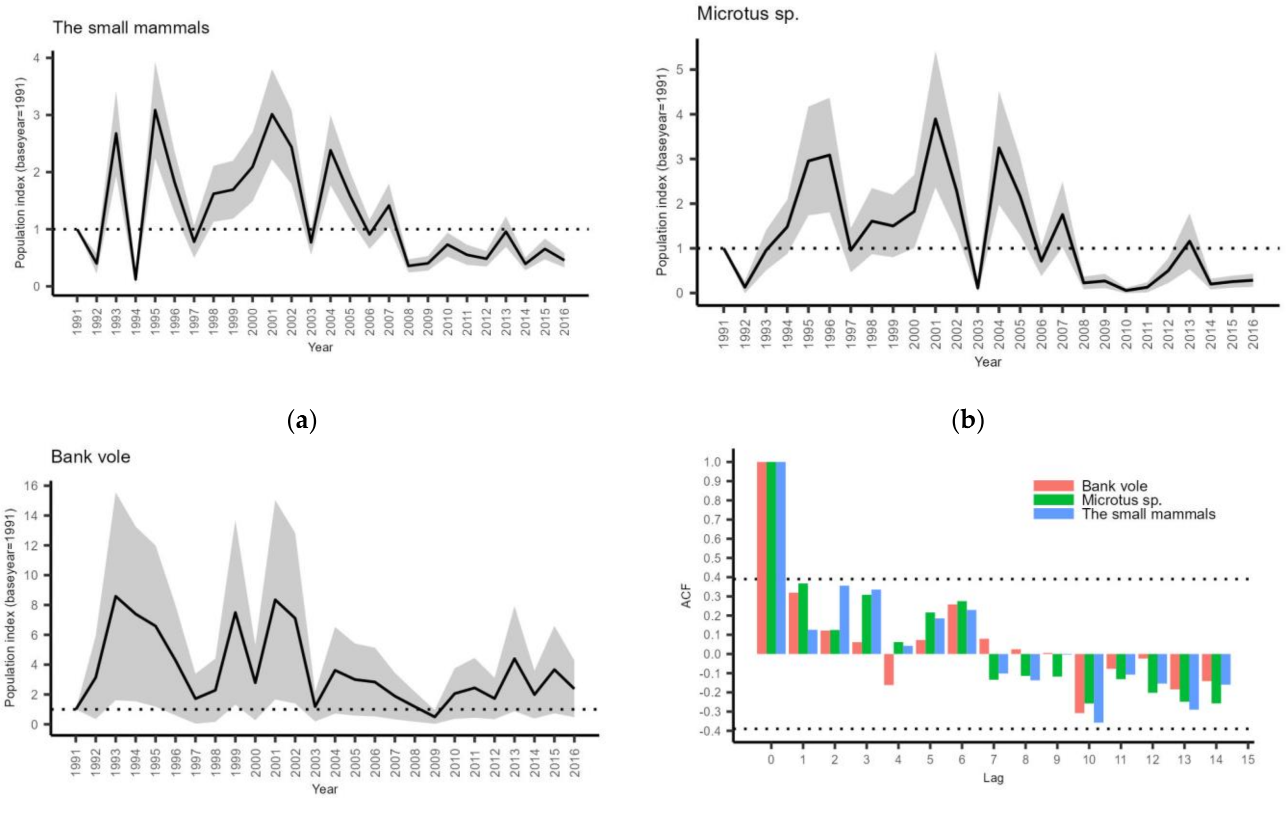
The number of small mammals per 100 trap-days over time in different sample areas and habitats is illustrated in Figure 2 (a). The figure shows that peaks and depressions well match between areas over time with only slight stochasticity between habitats within the same areas. This is confirmed by GLMM analysis showing no significant differences in marginal mean ratios of sample areas when accounting for individual transect in year Table A2. There are observable differences in the relative abundances of small mammals between habitats (Figure 2 (b)). GLMM analysis revealed meadow habitats having significantly lower abundances than any forest age group, but no differences between age groups (Table A3). Whereas comparison of fertility groups reveals meadows having significantly lower abundance and forests on fertile soils having significantly higher abundance after accounting for multiple comparisons (Table A4). In every comparison, GLMM including the hierarchical random intercept of transect in year and only the variable of interest in the fixed part, was the best performing model (with the lowest AICc values).



(**a**) (**b**)

Figure 2. Observed small mammal (pooled over species) population densities per 100 trap-days: (**a**) variation over time (1991-2016) in different sample areas and habitats; (**b**) observed number of the small mammals (per 100 trap-days) differences between habitats in time (2012-2016).

As we observed no meaningful differences between areas, we pooled all the results to construct population change analysis. All three models suggest statistically significantly declining population sizes (total number of small mammals S=0.9671±0.0083, p=0.0007; *Microtus* voles S=0.9306±0.0167, p=0.0005; bank vole *Clethrionomys glareolus* S=0.9706±0.0128, p=0.0325). Of course, small mammal population dynamics is not linear – yearly abundance indices are shown in Figure 3 (a-c).



(**a**) (**b**)

(**c**) (**d**)

Figure 3. Population indices with standard errors of: (**a**) the small mammals pooled; (**b**) voles of genus *Microtus*; (**c**) bank voles; and (**d**) Autocorrelation function analysis of the small mammal yearly indices, dotted lines indicate the threshold of significance.

Some cyclicity in population dynamics was apparent in the late 20th century and early 21st century but lost amplitude and frequency later (Figure 3 (a-c)). Since 2008, total number of the small mammals (Figure 3(a)) as well as *Microtus* voles (Figure 3 (b)) remained relatively stable and at low density level. The same happened with bank vole (Figure 3 (c)) earlier – around 2003. Graphical evaluation indicates a certain degree of matching between vole population indices in depression years, e.g., 1997, 2003, and to some extent also 2014 with overall moderate (r=0.5604) and statistically significant (t(24)=3.3146, p=0.0029) correlation. Autocorrelation function analysis shows no temporal cyclicity in any species group (Figure 3 (d)).

3.2. Owl breeding season diet

In total 164 STRALU samples from 86 different locations covering 23 years, 56 STRURA samples from 38 different locations covering 15 years, 24 ASIOTU samples from 21 different locations covering 9 years, 7 GLAPAS samples from 7 different locations covering 7 years and two AEGFUN samples from two different location covering two years (Figure 4, Table S1) were analyzed. The description of annual food composition per species is provided in Supplementary Table S1.

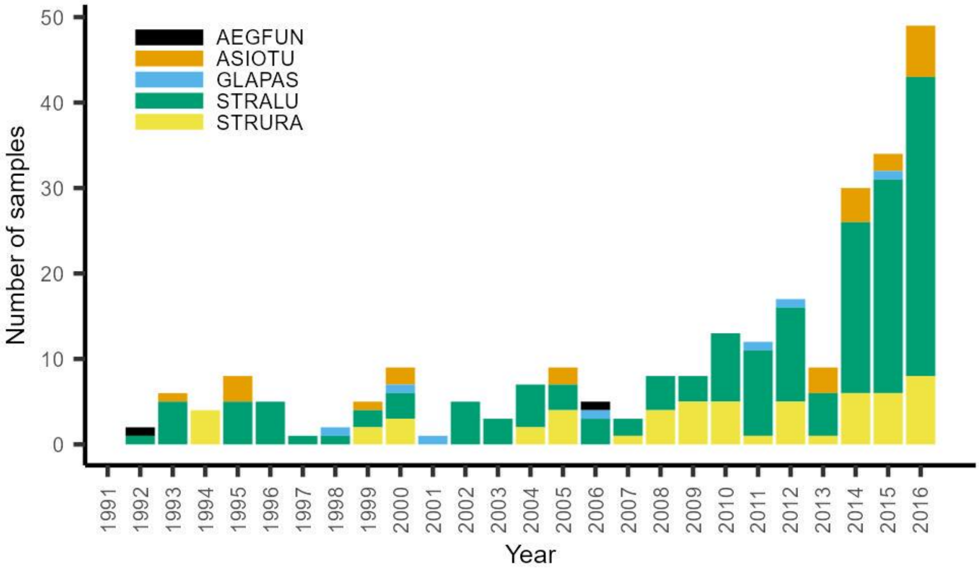
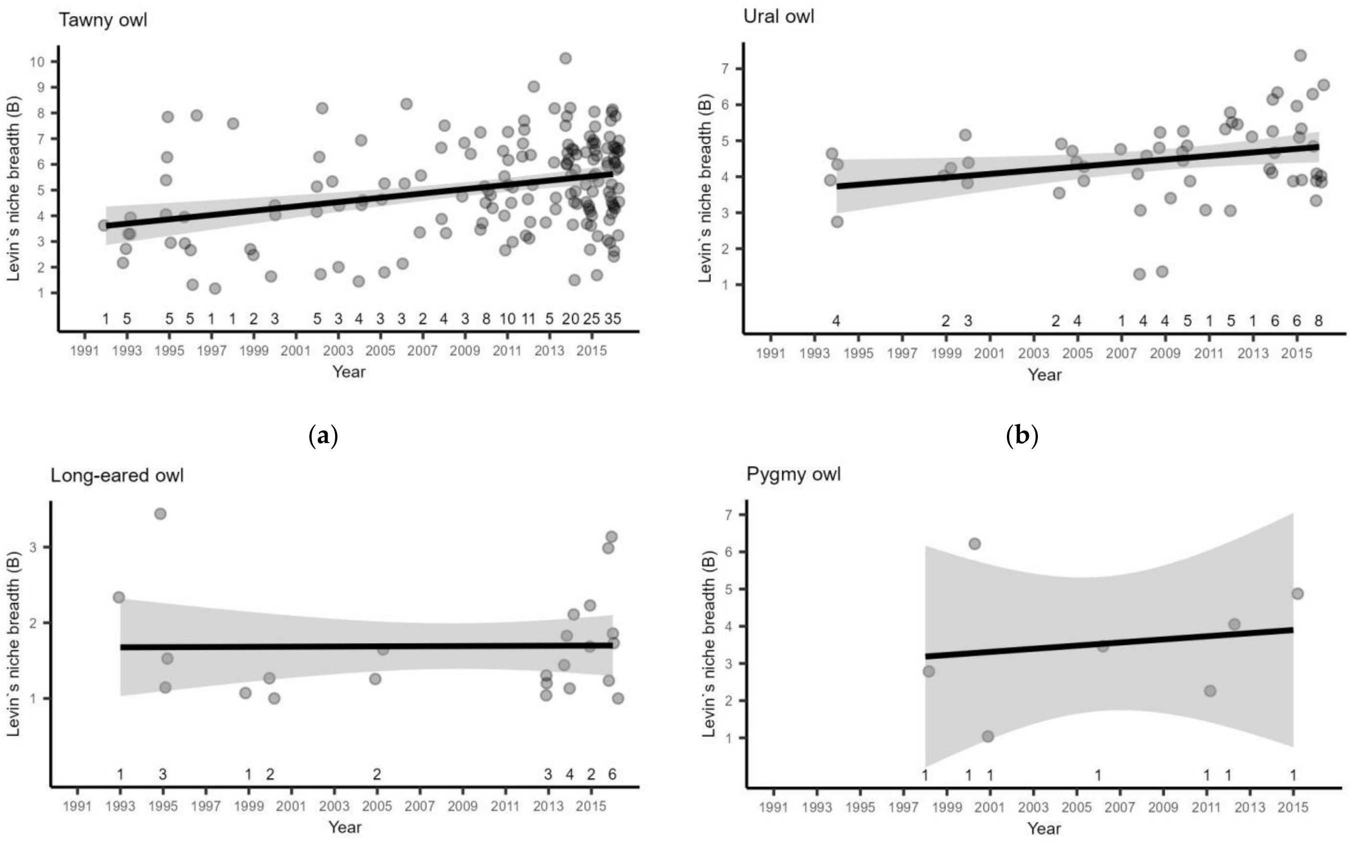


Figure 4. Number of owl diet samples (with at least 5 mammal individuals) over time.

The overall average food niche breadth of STRALU was 5.125 (95% bootstrapped confidence interval (bCI) 4.867-5.423). FNB increased significantly (β=0.0840±0.0198; t(129.2401)=4.249; p<0.0001) from 1992 to 2016. There are remarkable differences between samples in any given year (Figure 5 (a)), inclusion of nest ID as a random effect provides some help in dispersion taming (LMM: $R^2_{conditional}$=0.115, $R^2_{marginal}$=0.101, ICC=0.015) indicating some degree of territory specific variability. Even though the explained variances are low, we found a statistically significant negative effect of each of the small mammal population indices on FNB (Table 2). The proportion of voles (both groups) in owl prey statistically significantly positively correlated with their abundance indices, but species show preference for *Microtus* voles as their abundance index had a significant negative correlation with bank vole proportion in prey (Table 3). On average *Microtus* voles formed 15.55%, bank vole formed 5.51% and voles in total formed 31.65% of biomass.



(**a**) (**b**)

(**c**) (**d**)

Figure 5. Temporal change of Levin`s food niche breadth in four owl species: (**a**) tawny owl; (**b**) Ural owl; (**c**) long-eared owl; (**d**) pygmy owl. Grey points represent individual prey samples. The black line is the linear regression trend, and the grey ribbon is it`s 95% confidence interval. Numbers above the X-axis represent the number of samples. Y-axis range differs among the facets.

STRURA also showed large variability in the diet as overall FNB was 4.485 (95% bCI 4.201-4.758). We found a significant (β=0.0499±0.0227; t(54)=2.194; p=0.0325) increase in FNB from 1994 to 2016 (Figure 5). The overall variability is lower than in STRALU, but no nest specific intercepts were found to improve the model, and LM could explain only about 6.5% of the variance ($R^2_{adj.}$=0.06486). We found no correlation between FNB and small mammal population indices (Table 2). Species show a strong preference for *Microtus* voles, whose proportion in prey correlated positively with its abundance index, while higher abundance in nature led to a lower proportion of bank voles in prey (Table 3). As both vole abundance indices were correlated, we suggest preference as a reason for the negative correlation of the bank vole abundance index with its proportion in prey (Table 3). On average *Microtus* voles formed 15.10%, bank vole formed 6.07% and voles in total formed 31.78% of biomass.

Table 2. Description of prey abundance index influence on FNB per owl species.

Owl species	Prey (index)	β ± SE	Test statistic	df*	p-value	AICc	**$R^2_{adj.}$ / $R^2_{marg.}$	$R^2_{cond.}$	ICC
Tawny owl	Small mammals	-0.6127±0.1850	-3.312	144.778	0.0012	662.308	0.063	0.068	0.005
	Microtus voles	-0.3886±0.1551	-2.506	156.303	0.0132	667.001	0.037	0.049	0.013
	Bank vole	-0.2268±0.0812	-2.795	161.449	0.0058	666.913	0.046	0.052	0.007
Ural owl	Small mammals	-0.0039±0.2514	0.015	54	0.9880	177.536	-0.019		
	Microtus voles	-0.1304±0.1820	-0.716	54	0.4770	177.007	-0.009		
	Bank vole	-0.0050±0.0837	-0. 06	54	0.9520	177.532	-0.019		
Pygmy owl	Small mammals	-0.4948±0.7738	-0.639	5	0.5507	39.803	-0.109		
	Microtus voles	-0.5290±0.5286	-1.001	5	0.3628	39.075	0.0003		
	Bank vole	-0.4110±0.2885	-1.425	5	0.2136	37.967	0.147		
Long-eared owl	Small mammals	0.0171±0.1531	0.112	22	0.9120	56.975	-0.045		
	Microtus voles	-0.0672±0.1497	-0.449	22	0.6580	56.769	-0.036		
	Bank vole	0.0236±0.0752	0.314	22	0.7570	56.881	-0.041		

* Satterthwaite`s degrees of freedom in LMM.

** $R^2_{adjusted}$ reported in case of LM; $R^2_{marginal}$ in case of LMM.

The overall FNB of GLAPAS was 3.526 (95% bCI 2.355-4.756) and showed some temporal increase (Figure 5). However, this increase was not found to be statistically significant (LM: β=0.0420±0.1136, t(5)=0.369, p=0.727; $R^2_{adj.}$=-0.1681), probably due to high inter-sample variability and small overall sample size. We found no correlation between FNB and small mammal population indices (Table 2). Results on prey proportion with its relative abundance in nature are similar to STRURA, but the preference for *Microtus* voles is stronger, as that is a better explanator of bank vole proportion in prey (Table 3). On average *Microtus* voles formed 10.03%, bank vole formed 11.31% and voles in total formed 29.46% of biomass.

Table 3. Description of prey weight proportion in owl diet with its abundance index in nature (first two rows per owl species) or their cross-correlation.

Owl species	Prey (index)*	β ± SE	Test statistic	p-value	AICc	**R^2_{MF} / $R^2_{marg.}$	$R^2_{cond.}$	ICC
Tawny owl	Bank vole	0.0248±0.0057	4.359	<0.0001	5693.822	0.0005	0.134	0.133
	Microtus voles	0.1302±0.0061	21.520	<0.0001	14934.823	0.004	0.191	0.189
	Bank~*Microtus*	-0.0138±0.0116	-1.189	0.2340	5711.112	<0.0001	0.134	0.134
Ural owl	Bank vole	-0.1116±0.0072	-15.570	<0.0001	4693.187	0.0581		
	Microtus voles	0.1275±0.0100	12.720	<0.0001	6132.077	0.0268		
	Bank~*Microtus*	-0.1658±0.0175	-9.497	<0.0001	4865.001	0.0208		
Pygmy owl	Bank vole	-0.4168±0.0717	-5.812	<0.0001	261.048	0.178		
	Microtus voles	0.2136±0.0556	3.839	0.0001	220.591	0.073		
	Bank~*Microtus*	-0.9097±0.0811	-11.220	<0.0001	145.446	0.613		
Long-eared owl	Bank vole	-0.5294±0.0497	-10.640	<0.0001	761.318	0.215		
	Microtus voles	0.0611±0.0138	4.419	<0.0001	599.700	0.044		
	Bank~*Microtus*	-1.2718±0.1208	-10.530	<0.0001	705.794	0.276		

* Prey type Bank~*Microtus* represent proportion of bank voles in diet depending on *Microtus sp.* vole abundance in nature.

** $R^2_{McFadden}$ reported in case of GLM; $R^2_{marginal}$ in case of GLMM.

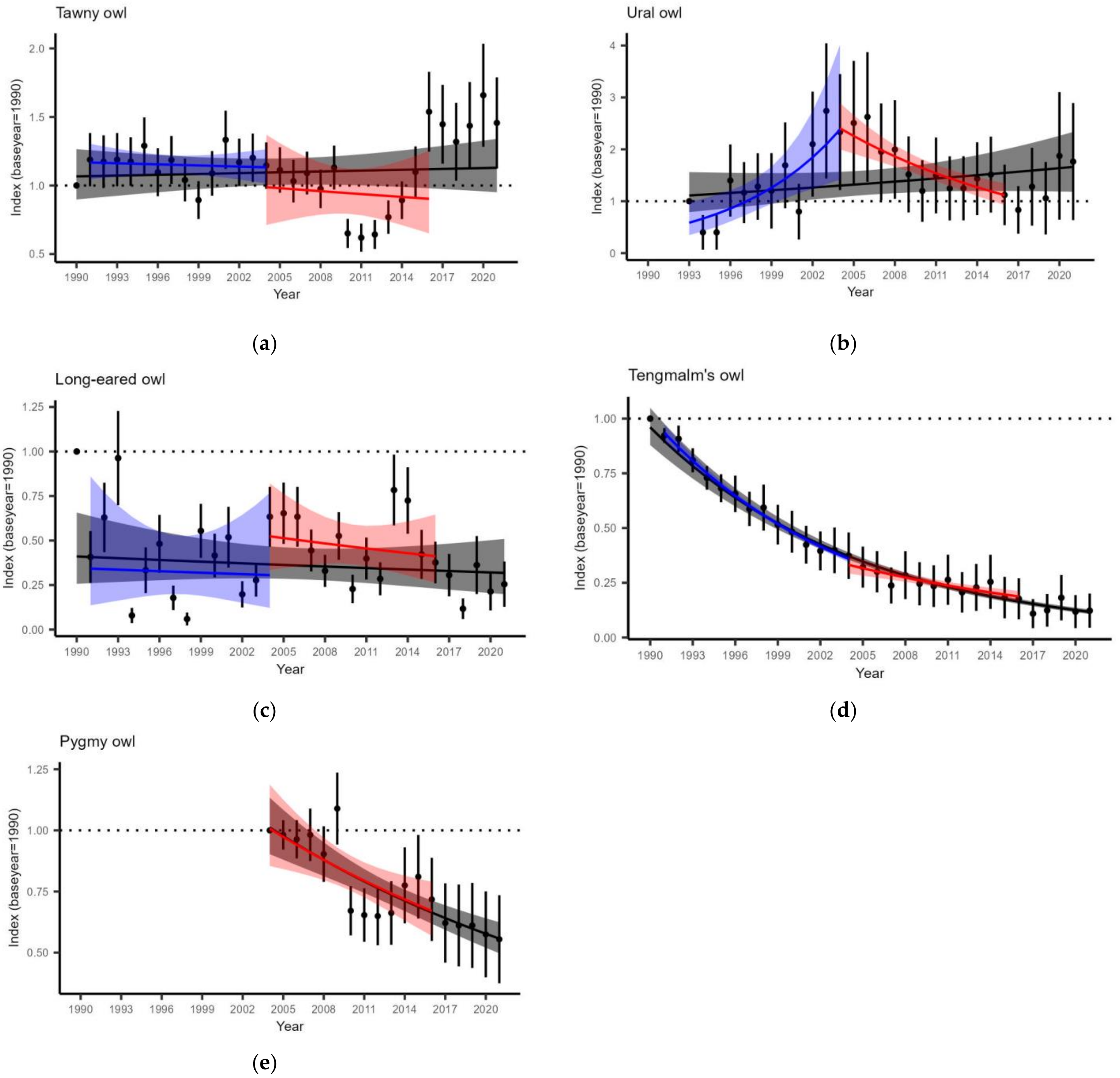
ASIOTU`s FNB is only 1.629 (95% bCI 1.429-2.002) and LM did not suggest any temporal change (β=0.0010±0.0176, t(22)=0.059, p=0.953; $R^2_{adj.}$=-0.0453). We found no correlation between FNB and small mammal population indices (Table 2). Species show a strong preference for *Microtus* voles over bank voles, and *Microtus* vole abundance in nature significantly correlated with its proportion in prey (Table 3). On average *Microtus* voles formed 71.18%, bank vole formed 4.64% and voles in total formed 87.13% of biomass.

The two analyzed samples of AEGFUN had FNBs of 1.588 and 4.318 (Table S1). On average *Microtus* voles formed 62.89%, bank vole formed 13.81% and voles in total formed 76.69% of biomass.

3.3. Owl population change

Our results differ between species when comparing owl population changes before and after the small mammal cycle depletion (Figure 6, Table 4).

STRALU with an overall (1990-2021) stable population (S=1.002±0.005), revealed no significant difference in population trajectories before and after depletion (Table 4). Even though the population experienced a considerable depression during 2010-2012, it has recovered since (Figure 6 (a)).



(**a**) (**b**)

(**c**) (**d**)

(**e**)

Figure 6. Population changes of owl species: (**a**) tawny owl; (**b**) Ural owl; (**c**) long-eared owl; (**d**) Tengmalm`s owl and (**e**) pygmy owl. Black dots with error bars are yearly indices with standard

errors, trend lines and ribbons with different colors represent different population trends: with black overall trend, with blue 1991-2004 and red 2004-2016. Y-axis range differs among the facets.

We obtained similar results for ASIOTU – overall (1990-2021) stable population (S=0.992±0.010) and no significant differences between periods (Table 4). However, a visual extension of the trend since mammal population depletion suggests a decline that might be obscured by fluctuating population (Figure 6 (c)).

The results of STRURA are different – although overall (1993-2021) population change classifies as stable (S=1.014±0.012), there are significant differences in trajectories (Table 4). Species had a strongly increasing population before 2004 and a steep decline since small mammal depletion (Figure 6 (b)).

GLAPAS had population change information only since the depletion, and overall (2004-2021) negative population trend (S=0.965±0.017) is similar to the one observed in 2004-2016 – significant decline (Figure 6 (e), Table 4).

The results for AEGFUN seem interesting as the overall (1990-2021) population had a steep decline (S=0.934±0.020), that fits estimated yearly indices (Figure 6 (d)). Nevertheless, the difference between slopes of "before" and "after" depletion is significant (Table 4) and suggests a steeper decline during the pronounced small mammal dynamics than since the depletion of cycles. Visually extending the trajectory of "after" similar pattern to "before" can be observed, thus the difference can be an artefact due to a higher influence of some years.

Table 4. Description of owl population change trends with small mammal cycles ("before") and since they vanished ("after"). Model coefficients are in log-odds scale.

Owl species	Parameter	β ± SE	Test statistic	p-value	df*	$R^2_{adj.}$ **
Tawny owl	Intercept	0.1178±0.0396	2.978	0.0062	26	-0.1096
	Time	0.0016±0.0043	0.368	0.7159		
	Before			reference		
	After	<0.0001±0.0059	<0.0001	1		
	Time:After	<0.0001±0.0006	<0.0001	1		
Ural owl	Intercept	0.1389±0.1361	1.020	0.319	21	0.5837
	Time	0.0319±0.0179	1.783	0.089		
	Before			reference		
	After	1.1350±0.1925	5.898	<0.0001		
	Time:After	-0.1354±0.0253	-5.361	<0.0001		
Pygmy owl***	Intercept	0.0069±0.07470	0.093	0.9279	11	0.4368
	Time	-0.0339±0.0106	-3.210	0.0083		
Long-eared owl	Intercept	-0.8450±0.2688	-3.144	0.0046	23	-0.0302
	Time	-0.0143±0.0328	-0.436	0.6666		
	Before			reference		
	After	0.3087±0.3801	0.812	0.4250		
	Time:After	-0.0080±0.0464	-0.172	0.8651		
Tengmalm`s owl	Intercept	-0.5246±0.0331	-15.855	<0.0001	23	0.9740
	Time	-0.0607±0.0040	-15.033	<0.0001		
	Before			reference		
	After	-0.7508±0.0468	-16.043	<0.0001		
	Time:After	0.0183±0.0057	3.211	0.0039		

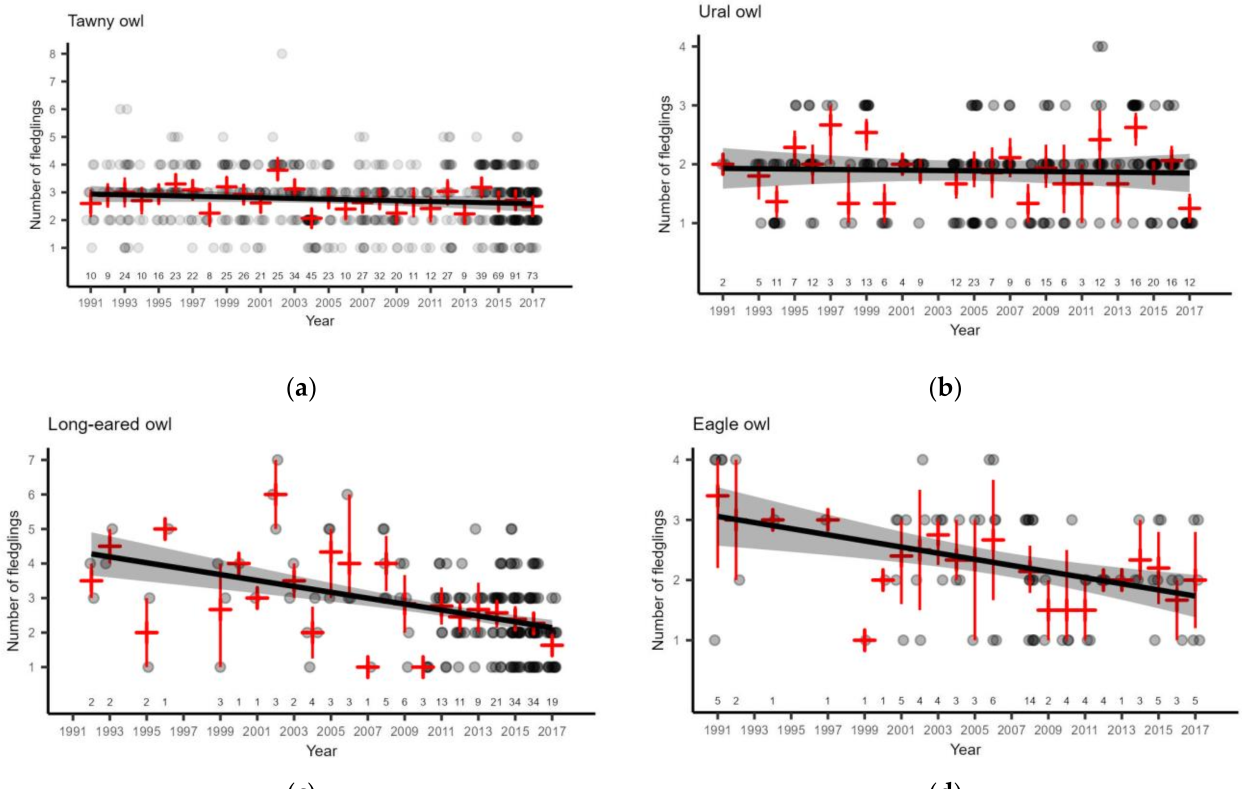
* df are the same in each variable.

** values represent whole model.

*** Pygmy owl had only data since 2004.

3.4. Owl breeding performance

On average STRALU had 2.32 (95% bCI 2.23 – 2.40, n=934) fledglings per successful nest. Even though it appears to have had reduced breeding performance since 2004 (Figure 7 (a)), these differences are not statistically significant (Table 5). The overall trend of breeding performance was insignificant (β: -0.0041±0.0088, t(26)=-0.467, p=0.645; $R^2_{adj.}$=-0.0298; F(1;26)=0.2179, p=0.6445). We did not find a correlation with the small mammal abundance indices in the year of breeding or the previous autumn (Table 6).



(**a**) (**b**)

(**c**) (**d**)

Figure 7. Annual number of fledglings of four owl species: (**a**) tawny owl; (**b**) Ural owl; (**c**) long-eared owl; (**d**) eagle owl. Grey points represent individual nest performance. Red crosses are bootstrapped 95% confidence intervals around the annual mean value. The black line is the linear regression through mean values and the grey ribbon is it`s 95% confidence interval. Numbers above X-axis represent annual number of samples. Y-axis range differs among the facets.

On average STRURA had 1.69 (95% bCI 1.58 – 1.80, n=280) fledglings per successful nest. Even though it appears to have had some differences in trends of breeding performance before and after small mammal cycle dampening (Figure 7 (b)), they are not statistically significant (Table 5). The overall trend of breeding performance was insignificant (β: -0.0014±0.0122, t(24)=0.112, p=0.912; $R^2_{adj.}$=-0.0411; F(1;26)=0.0125, p=0.912). We did not find correlations with the small mammal abundance indices in the year of breeding or the previous autumn (Table 6).

The average number of fledglings of ASIOTU was 2.54 (95% bCI 2.38 – 2.72, n=189) fledglings per successful nest. However, this population parameter declined over time (Figure 7 (c)) by approximately one fledgling in 16 years (β: -0.0627±0.0297, t(22)=-2.109, p=0.0466; $R^2_{adj.}$=0.1303; F(1;22)=4.446, p=0.0466). We did not find a correlation with the small mammal abundance in the year of breeding or the previous autumn (Table 6).

Table 5. Description of owl breeding performance trends with small mammal cycles ("before") and since their depletion ("after").

Owl species	Parameter	β ± SE	Test statistic	p-value	df*	$R^2_{adj.}$ **
Tawny owl	Intercept	2.6221±0.1594	16.452	<0.0001	23	0.0765
	Time	0.0174±0.0194	0.896	0.380		
	Before			reference		
	After	-0.3597±0.2254	-1.596	0.124		
	Time:After	0.0216±0.0275	0.784	0.441		
Ural owl	Intercept	1.8291±0.1709	10.705	<0.0001	21	-0.0812
	Time	0.0106±0.0224	0.473	0.641		
	Before			reference		
	After	-0.2022±0.2416	-0.837	0.412		
	Time:After	0.0293±0.0317	0.923	0.366		

* df are the same in each variable.

** values represent whole model.

The average number of fledglings of BUBBUB was 2.26 (95% bCI 2.04 – 2.46, n=81) fledglings per successful nest. This population parameter declined over time (Figure 7 (c)) by approximately one fledgling in 22 years (β: -0.0450±0.0137, t(20)=-3.293, p=0.0036; $R^2_{adj.}$=0.3191; F(1;20)=10.840, p=0.00036). We found positive correlations with the abundance index of pooled small mammals in the breeding season and the previous autumn, with a stronger effect of the latter (Table 6). The effect of the *Microtus* vole abundance index in the previous autumn was also statistically significant and positive (Table 6).

We had too few reliable observations of GLAPAS and AEGFUN breeding performance for analysis, therefore we provide only a description of the average values: respectively 2.75 (95% bCI 2.00 – 3.50, n=8) and 1.75 (95% bCI 0.50 – 2.75, n=4).

Table 6. Spearman`s correlation analysis results of the annual mean number of fledglings and small mammal abundance indices in the year of breeding and the year before (annotated as $^{-1}$).

Owl species	Prey (index)	r_s	p-value	Number of years	S
Tawny owl	Small mammals	-0.1152	0.5737	26	3262
	Microtus voles	-0.1391	0.4962	26	3332
	Bank vole	0.0338	0.8700	26	2826
	Small mammals^{-1}	0.1300	0.5341	25	2262
	Microtus voles^{-1}	0.1377	0.5100	25	2242
	Bank vole^{-1}	0.1946	0.3496	25	2094
Ural owl	Small mammals	-0.0179	0.9340	24	2341.1
	Microtus voles	0.0545	0.8005	24	2174.8
	Bank vole	-0.0863	0.6886	24	2498.4
	Small mammals^{-1}	-0.1788	0.4145	23	2385.8
	Microtus voles^{-1}	-0.2104	0.3351	23	2449.9
	Bank vole^{-1}	0.0218	0.9214	23	1979.9
Long-eared owl	Small mammals	0.0805	0.7755	15	514.92
	Microtus voles	0.1252	0.6566	15	489.87
	Bank vole	0.0787	0.7804	15	515.92
	Small mammals^{-1}	0.3062	0.2871	14	315.69
	Microtus voles^{-1}	0.0529	0.8576	14	430.95
	Bank vole^{-1}	-0.2643	0.3612	14	575.26
Eagle owl	Small mammals	0.5329	0.0408	15	261.59
	Microtus voles	0.3817	0.1604	15	346.28
	Bank vole	0.3402	0.2146	15	369.49
	Small mammals^{-1}	0.6438	0.0130	14	162.09
	Microtus voles^{-1}	0.5527	0.0404	14	203.50
	Bank vole^{-1}	0.2020	0.4886	14	363.09

$^{-1}$ abundance index in previous autumn.

4. Discussion

4.1. Small mammal monitoring

Overall the small mammal densities and trapping indices in our study (Figure 2) are similar to findings in the neighboring countries - Estonia [16, 76] and Lithuania [77-79]. We found meadow habitats to have lower abundance of small mammals than forests (Table A3, Table A4). These are similar results to Estonia [16] and Lithuania [78], where increasing small mammal abundance was recorded with increasing forest age in early meadow-forest succession. We found statistically significant differences between the forest soil fertility classes (Table A4), but, due to large within-class variation we did not find clear differences between age groups (Table A3). In Estonia, forest age was found to be an important explanatory variable for small mammal abundance [16]. Study in Finland [80] found mature forests to hold the highest abundance of voles. Overall similar results were found in a long term study in southeastern Norway, besides highlighting importance of mature forests as areas containing relatively high abundances even during the depression of the small mammal populations in late 20th century [81]. Whereas a study in northern Sweden suggests young stands to have higher small mammal diversity and abundance if large amount of felling remains is left [82]. Many authors found that high vegetation complexity, habitat structural diversity and abundance of coarse woody debris are important factors, that can ensure high small mammal species diversity and abundance also in young stands and unmanaged habitats under natural succession [79, 81-85]. The negative effects of intensive forestry were found to be important also at the landscape scale [83-86]. Though in mosaic landscape, ecotones (with at least 100m buffer zone of habitat edges) were found to contain highest small mammal density and diversity [77, 81, 84]. In our study, we found cases of some declines in the small mammal numbers linked to forestry activities but unrelated to changes in other transects (Figure 2). The insufficient number of transects and occurrences did not allow for statistical testing of forestry impacts. Most of the small mammal monitoring transects are in intensively managed forests, thus under the influence of landscape management. Yet two of the longer-term areas are in protected areas (Apasalas and Žūklis), suggesting larger, than local (or management) effects on the dampening of the cycles.

One of the most robust explanations of cyclicity was provided by Hanksi *et al.* [17] with further extensions for different systems (see [87] for overview). One of those extensions, modelling multispecies rodent assemblages, found transient dynamics that alternated between long time periods with cyclic and non-cyclic fluctuations [19]. These fluctuations were expected to cover relatively small spatial scales, yet the phenomenon of dampened cycles was more recently found to be Europe-wide [25], suggesting broader environmental drivers, for example, climate change [22-23]. However, in some parts of Europe, the period of dampened vole population cycles was shorter, than in others, refuting the generality of climate forcing hypothesis [26]. Our results also show clearly dampened vole cycles in Latvia (Figure 3 (a-c)) – an event, that was not reported in neighboring counties [14-16], suggesting some smaller scale processes as described by predator-prey models. Even though Hanski`s *et al.* models were created for Fennoscandian environment, their generality was shown also in central and western Europe [13]. According to these models and previous studies (see [87] for an overview), generalist predators tend to stabilize rodent dynamics and nomadic avian predators have similar effect on rodents, but they also increase the regional synchrony. Whereas specialist predators were thought to maintain the fairly regular rodent cycles, but see again [19].

4.2. Numerical response of owls

We found statistically significant relationship between proportion for voles (*Microtus* and bank voles) in owl diet and their relative abundance indices in nature (Table 3). This means, even though, we used mammal abundance information from autumn, it is still able to represent the use of them in owl prey. It is known that small mammal densities increase during summer [52] and spring count represent winter survival and reproduction [88], but relative value of the year (spring or autumn) still represent part of the cycle in cyclic environments [41]. We found preference for *Microtus* voles in every species analyzed, these voles also had higher biomass proportion than bank voles (Table 3). Generally higher proportion of *Microtus* voles than bank voles in owl diet can be related to different breeding biology and dispersal between groups and predator escaping behavior (see [19] for an overview).

4.2.1. Long-eared owl

We found ASIOTU to have the narrowest food niche breadth from investigated species. The calculated values are lower than in Lithuania [28], possibly due to pooling of the results to genera level. Species is known to be small mammal specialist in Europe [27] with high proportion of *Microtus* voles in the diet [28, 89-93]. ASIOTU has a strong functional response to vole abundance [29, 30, 42, 94]. It is suggested that species can adapt migratory behavior and breeding region selection during migration accounting for vole abundance [95]. And it may even have repeated breeding attempts if the vole abundance is high [96-97].

The average breeding performance in Latvia is similar to 2.94±0.42 (μ±SD; n=1339) in Finland [98] and 2.39 (n=72) in the United Kingdom [96]. We observed significant decline in the number of fledglings per successful nest - more than one chick in three generations (5.7 years; [99]). The steepest decline is in the last two generations and matches the time of dampened populations of the small mammals (Figure 7 (c)). The declining breeding performance did not have an impact on the population change (2004-2016), but extension of the trend (2004-2021) shows significant decline (β: -0.0530±0.0191, t(16)=-2.772,

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p=0.0136). We consider that for a longer period of time, ASIOTU population was supported by immigration of migrating individuals hatched elsewhere [29, 90, 100-101] and later decline implies a delayed response of returning individuals of Latvian origin. Stronger site fidelity is observed in regions where species is resident [91, 102], but in Latvia there is low variability of territory occupancy in the sample areas (authors' personal observations).

As species shows no strong territorial defense and hunting grounds may largely overlap between neighboring pairs [102-103], habitat composition and prey abundance are found to be the most important factors shaping local ASIOTU populations [90, 104-106]. We found no correlation between the breeding performance and prey abundance indices in the year of breeding nor the year before (Table 6). It is likely due to selection of breeding territories with sufficient abundance of the prey. This is supported by the knowledge of species benefitting from relatively small landscape elements, for example, flower strips [104]. Therefore, we consider agri-environmental schemes with ecological compensation areas in farmlands an important tool for conservation of the species.

4.2.2. Tengmalm's owl

Even though we have only two samples of AEGFUN diet, its FNB suggests high specialization, which is supported by a high proportion of voles in the diet. The observed proportions in Europe show high importance of voles (overview in [32]), averaging on 54.89% of items through studies. Species has strong functional response to vole abundance influencing habitat selection via hunting behavior [47, 107-109], the timing of breeding and breeding performance [6, 39] and survival [39, 43]. Even with a certain degree of carry-over effect, species shows strong adaptability to fluctuating food conditions in terms of breeding performance [110].

The average long-term number of fledglings in Finland is 4.04±0.62 (μ±SD; n=13817) [110] and around 2 fledglings per successful nest in poor vole years [32, 111]. The scarce available data on the breeding performance in Latvia suggests that it is similar to vole depression years in Finland.

We found steep decline of AEGFUN population throughout the studied period (Figure 6(d)), but it was slower with depleted population dynamics of the small mammals (Table 4). We expected this to be an artefact of some better seasons or immigration from Fennoscandia and Russia [32], rather than actual difference, therefore, we extended the period of analysis in then"after" group. Our results (β: -0.0618±0.0074, t(16)=-8.302, p=<0.0001) showed the decline since 2004 closely matching the overall population decline and the slope of the period with pronounced population dynamics of the small mammals. Some researchers have hypothesized of potentially negative effects of increasing STRURA population on the population of the AEGFUN [32]. But we did not find any AEGFUN as a prey of STRURA, even though superpredation is known [34], and both species coexist in the same study areas (authors' personal observations). Even more, in central Europe, breeding in proximity of STRURA is found to protect AEGFUN against STRALU [112-114].

Population declines are reported also in Finland, Sweden and Estonia [115], suggesting a larger-scale factors affecting the population. Species is a mature spruce and mixed forest specialist [47, 105, 109, 116-119]. These are habitats with some of the highest densities of the small mammals [79-85]. We consider the loss of species-specific habitats to be the most important factor in population decline, amplified by dampened dynamics of the small mammal populations in Latvia. The forestry intensity, measured by tree cover loss, is increasing in Latvia and, in particular, in priority sites for species conservation [122].

4.2.3. Eurasian pygmy owl

We found average level of specialization of GLAPAS with the strongest preference for *Microtus* voles from the analyzed owl species (Table 3), though with low proportion of

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voles in the diet. The vole proportion is similar to breeding season diet in Finland [34] and in central Europe [123]. Masoero *et al.* found strong numeric and functional response of GLAPAS to vole abundance in winter [33], suggesting not only age and gender specific preference to voles, but also stronger migratory behavior during low vole density years in boreal Finland. During higher vole population densities, also breeding density and performance of GLAPAS increase [6, 124]. The dependency on voles was found to be stronger in boreal, than boreonemoral region, with breeding both in low and peak vole years in the latter [40]. In the boreonemoral zone the onset of breeding was later with no correlation with breeding performance and the clutches were slightly smaller than in the boreal zone [40].

For the few documented records of successful breeding in Latvia, the values are markedly lower than 5.85±0.55 (μ±SD; n=13817) in Finland [98] and boreal Norway (6.9±1.1) and somewhat lower than in boreonemoral Norway in vole crash years (3.7±2.8) [40]. The difference with boreonemoral Norway indicates possible cumulative effect of longer-term dampened population cycles of the small mammals and is supported by declining GLAPAS population. The population in Estonia and Lithuania is increasing [115], but it is declining in Latvia (Figure 6(e) and Table 4) and in Finland [98, 115]. It has to be highlighted, that only Finland and Latvia were able to provide analytical assessment of the population (type: interval) in the last article 12 report of the Birds Directive [115], therefore it cannot be ruled out, that the increase in the other Baltic states is more based on increased survey efforts and knowledge than a genuine change. Even though irruptions linked with low rodent availability occur from time to time [125], it is unlikely to assume Finland and Latvia being a source population for neighboring countries with declining populations themselves even with the increased distribution of the species [51]. This can be supported by similar pattern of yearly indices in Latvia (Figure 6 (e)) and Finland [98], but with steeper decline in Latvia.

GLAPAS is known to be a structurally rich mature spruce and mixed forest specialist species during the breeding season [124, 126-133], and clearcuts and logging are shown to affect habitat suitability [133] as well as population size [134]. Structurally rich mature forests are habitats with some of the highest densities of the small mammals [79-85, 135]. Both Latvia and Finland are countries in Europe with the highest forestry activity even in protected areas [136]. We consider the loss of species-specific habitats to be the most important factor in the population decline, amplified by the dampened dynamics of the small mammal populations in Latvia. The forestry intensity, measured by tree cover loss, is increasing in Latvia and, in particular, in the priority sites for species conservation [122].

4.2.4. Ural owl

One of the highest and temporarily increasing FNB was found in STRURA. We found a relatively low proportion of voles in the species diet. This proportion, when compared by count is lower than in Finland [34-35,137-138], similar to Belarus [139-141] and higher than in Slovenia [35]. When comparing the food niche as a whole, STRURA diet in Latvia was found to be similar to the one in Finland during low vole phase [35]. Even though the species is known to be a generalist predator, strong functional response to vole abundance is proven in Fennoscandia, ranging from the timing of breeding and breeding performance [3, 6, 39, 41, 142] to winter survival [3, 6, 39, 41, 45] and even demonstrating a carry-over effect from the previous year ([48]) and a change in behavior [46, 143-144].

Not only the food niche but also the breeding performance of STRURA in Latvia is similar to Finland in bad vole years. In Latvia we observed on average 1.69 (95% bCI 1.58 – 1.80, n=280) fledglings per successful nest and no temporal trend. Overall corresponding value in Finland (1986-2016) is 2.59 (±0.43 SD, n=18901; [98]) and between 1.3 and 2 [3, 41] in bad vole years, roughly matching our results. Given the strong numerical response to voles, we expected declining trend in breeding performance, but we did not find it. We consider this as an example of strong parental investment [144-146] by adjustments in hunting activity, and possibly habitat selection [105], demonstrating the high plasticity of the species [35]. As Figure 2 shows, even with dampened small mammal cycles, there are habitats with high prey abundance, thus allowing to meet the prey demands of the young. The size of nest-boxes in Latvia is similar to Finland [35] and cannot be suspected as a reason for lower breeding performance.

Increasing STRURA populations and expanding range, even increasing the niche of utilized habitats was observed in many parts of Europe during the first decade of the 21st century [147-150]. This overlaps with increase also in Latvia, and breeding occurrences in a mosaic landscape [105]. Given the extent of population increase, some unknown large-scale factors are most likely to be the explanation. Nevertheless, in Latvia the period of steep decline of the species population overlapped with the dampening of the small mammal population dynamics. We consider the relative abundance of the small mammals to be an important collider to overall habitat change as species ecological niche analysis in Latvia suggest strong dependency on large forest massifs with dominance of mature forests and only some openings [105]. These are habitats found important for the species also elsewhere [148, 151-152]. Even though the range is still expanding in Latvia [153], the overall population size is declining [115]. The forestry intensity, measured by tree cover loss, is increasing in Latvia and, in particular, in priority sites for species conservation [122]. We consider this as an argument for the conservation of mature forests important for the species and holding higher densities of its main prey – the small mammals [81].

4.2.5. Tawny owl

The highest FNB value was found in STRALU with a relatively low proportion of voles in diet. The average FNB value was slightly lower than in Lithuania [28]. We observed a temporal increase in FNB, that is similar to observation in Lithuania with a declining proportion of *Microtus* voles [36]. Species is known to be a generalist feeding on the available prey with no particular preferences [154]. The food composition can highly vary between breeding regions within the same year and between years in the same breeding territory [28, 36, 154-162]. Nevertheless, in the cyclic environment of Fennoscandia a strong numerical response to vole abundance was found, including the timing of breeding [6, 162], breeding performance ([3, 5, 6, 39, 162] and winter survival [3, 39].

Both the population change, and breeding performance of STRALU were stable and showed no differences with pronounced and dampened vole cycles. Breeding performance is lower than 3.26±0.41 (μ±SD; n=9668) in Finland, where the population is also stable [98]. And lower than in Lithuania, where an increasing trend of breeding performance (2002-2014) was observed and co-occured with decline in number of breeding pairs [36]. We consider the relatively low breeding performance in Latvia related to the high population density – estimated around 16 604 in Latvia and below 4000 in Lithuania [115]. Observed depression of STRALU population from 2010 to 2012 in Latvia partially matches with Lithuania [36]. We consider this to be a consequence of two consecutive snow-rich winters with multiple freeze-thaw events forming ice sheets in snow cover – factors reducing species survival [45, 164-165]. This event did not affect breeding performance and the population recovered quickly.

We think that the quick population recovery and overall stable breeding performance even with increasing FNB values was possible due to the breeding habitat availability. Even though, species is well known generalist breeding from cities to large forest massifs in more southern latitudes [34], in boreonemoral region species preferred forest edges over the interior [105, 166]. But with increasing forestry and forest fragmentation more suitable landscape for the species is created [105], probably overwhelming the negative effects of the depleted small mammal populations.

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4.2.6. Eagle owl

The largest European owl species the eagle owl is known to be a generalist predator with the proportion of rodents in diet ranging from 0 to 97.7% with average of 49.7% from 182 studies (overview in [37]). We do not have reliable information on the diet of BUBBUB in Latvia, but during the ringing of the young a lot of bird feathers are found, as most of the known breeding sites are in a close proximity to waterfowl lakes and landfills [105]. The species is resident with no known seasonal migrations in Europe [37, 167] and breeding dispersal occurs mostly due to the loss of a mate [37]. As lakes are under an ice cover and most of the waterfowl and gulls in Latvia are migrants [153], it is likely that BUBBUB is highly dependent on voles, at least in winter. This is supported by a study in Finland evaluating the robustness of the alternative prey hypothesis of BUBBUB [168]. The study found correlation between vole abundance in nature and their proportion in diet, and the proportion of alternative prey to be nearly independent of its abundance in the field [168]. There are several other studies highlighting the high proportion of voles in the BUBBUB diet [169-171].

The overall average number of fledglings per successful nest in Latvia is similar to Europe – around 2 (overview in [37]). But we have observed a declining trend with a loss of more than one fledgling in two generations (generation length is 12.1 years; [172]). We found breeding performance correlated with the abundance index of the small mammals in field and the correlation was stronger with the value from the previous autumn (table 6). Larger broods and earlier breeding was found in BUBBUB pairs with a diet based on high-value foods (rabbits and rodents) [173-174] and higher productivity associated with higher proportion of the main prey in diet [175]. We cannot relate breeding performance with the diet, but we consider the negative effect of a reduced abundance of the small mammals to highlight a carry-over effect, influencing adult fitness in spring and thus reducing the breeding performance. This phenomenon is well known in STRURA [41, 48, 143, 176-177] and proven to be of increasing importance with the size of an owl species in Finland [6]. Ecological niche analysis in Latvia also suggests the importance of habitats with higher vole abundance [81] for BUBBUB [105].

Even though we have a limited number of nests known annually, they form an important part of the whole population estimated around 24 breeding territories and the national population trend is declining [115]. We consider our findings of possible carry-over effect important in species conservation and linked to population decline via reduced breeding performance and likely also reduced winter survival as both should be related via fitness, though it needs to be studied more directly. Nevertheless, we consider conservation of habitats important for breeding and winter feeding together with nest site protection from ground predators necessary to reduce the effects of dampened population dynamics of the small mammals.

5. Conclusions

1. Small mammal relative abundance indices show depleted population cycles since approx. 2004, but in some forest habitats the relative densities are still high. We found no differences between trapping indices in different parts of Latvia; therefore, we conclude them to be a part of the same dynamics at least in the eastern part of the country.

2. We found a significantly declining number of fledglings of ASIOTU since the depletion of the small mammal dynamics. The population size of the species declined later and was significant for the period from 2004 to 2021. ASIOTU is the most specialized from the analyzed species on voles in the diet.

3. Breeding performance of three forest specialist species AEGFUN, GLAPAS and STRURA in Latvia is similar to vole depression years in boreal and boreonemoral region. We did not detect temporal trend of breeding performance in STRURA, even in the presence of increasing food niche breadth.

4. Populations of pygmy and AEGFUN are declining in Latvia and showed no difference in respect to compared periods with pronounced or depleted population dynamics of the small mammals. In contrast, population size of STRURA showed signifi-

cant decline since rodent depression. We consider the depletion of the small mammal population dynamics to be an important negative contributing factor to more important effects of forestry.

5. Neither breeding performance nor population size of STRALU changed between the compared periods with pronounced and depleted population dynamics of the small mammals. This suggest strong plasticity of the species as food niche breadth was temporarily increasing.

6. We found evidence that might suggest dependency of BUBBUB on voles via a carry-over effect. The breeding performance of BUBBUB is significantly correlated with the abundance indices of the small mammals in nature in previous autumn.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: Description of owl diet per year; Table S2: Population indices of the small mammals; Table S3: Population indices of owls; Table S4: Description of owl breeding performance.

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Institutional Review Board Statement: Ethical review and approval were waived for this study as nest visits were performed by professional ringers, owl census and small mammal monitoring was performed following monitoring methods approved by Nature Conservation Agency and in conjunction with them.

Data Availability Statement: The aggregated (per species per year) data presented in this study are available in the supplementary material of this article. The raw data are not publicly available as we are not allowed to share raw monitoring information or nest locations.

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Appendix A

Table A1. Minimum legal rotation ages per site quality class in main tree species. Currently, there is no minimum rotation age in grey alder. We used 35 years, as it is the age of the youngest stand registered as "full grown" in FSR

Dominant tree species	Highest quality	Medium quality	Lowest quality
Oaks	101	121	121
Pines and larches	101	101	121
Spruces, ashes, limes, elms, maples	81	81	81
Birches	71	71	51
Black alder	71	71	71
Aspens	41	41	41

Table A2. Marginal means comparison (tests are performed on the log-scale; p-adjusted by Tukey`s method) between sample areas. Model with random intercept per transect and main effects of sample area and year was considered the best*.

Sample Areas contrasted	Ratio ± SE	z-ratio	p-value
Apsalas/Augstroze	0.704 ± 0.459	-0.538	0.9983
Apsalas/Kaunata	0.468 ± 0.307	-1.157	0.9099
Apsalas/Ķemeri	1.816 ± 1.587	0.682	0.9936
Apsalas/Lubāna	0.538 ± 0.35	-0.951	0.964
Apsalas/Pļaviņas	0.566 ± 0.371	-0.868	0.9772
Apsalas/Žūklis	1.329 ± 1.176	0.322	0.9999
Augstroze/Kaunata	0.665 ± 0.236	-1.148	0.9132
Augstroze/Ķemeri	2.578 ± 1.752	1.393	0.8057
Augstroze/Lubāna	0.764 ± 0.265	-0.774	0.9874
Augstroze/Pļaviņas	0.804 ± 0.286	-0.614	0.9964
Augstroze/Žūklis	1.887 ± 1.308	0.917	0.9701
Kaunata/Ķemeri	3.877 ± 2.65	1.983	0.4257
Kaunata/Lubāna	1.149 ± 0.408	0.393	0.9997
Kaunata/Pļaviņas	1.209 ± 0.439	0.522	0.9985
Kaunata/Žūklis	2.839 ± 1.978	1.498	0.7465
Ķemeri/Lubāna	0.296 ± 0.201	-1.79	0.5547
Ķemeri/Pļaviņas	0.312 ± 0.213	-1.705	0.6123
Ķemeri/Žūklis	0.732 ± 0.663	-0.344	0.9999
Lubāna/Pļaviņas	1.052 ± 0.373	0.142	1
Lubāna/Žūklis	2.47 ± 1.711	1.305	0.8498
Pļaviņas/Žūklis	2.349 ± 1.633	1.228	0.8834

* AICc=1603.663, $R^2_{conditional}$=0.877, $R^2_{marginal}$=0.177, ICC=0.851.

Table A3. Marginal means comparison (tests are performed on the log-scale; p-adjusted by Tukey`s method) between forest age classes. Model with random intercept per transect and main effects of forest age class and year was considered the best*.

Forest age groups contrasted	Ratio±SE	z-ratio	p-value
Young/meadow	7.078 ± 2.772	4.997	<.0001
Young/Medium	1.458 ± 0.442	1.244	0.599
Young/Old	1.627 ± 0.477	1.661	0.3446
meadow/Medium	0.206 ± 0.073	-4.451	0.0001
meadow/Old	0.23 ± 0.079	-4.257	0.0001
Medium/Old	1.116 ± 0.27	0.452	0.9692

* AICc=1579.355, $R^2_{conditional}$=0.884, $R^2_{marginal}$=0.409, ICC=0.804.

Table A4. Marginal means comparison (tests are performed on the log-scale; p-adjusted by Tukey`s method) between soil richness classes. Model with random intercept per transect and main effects of soil fertility class and year was considered the best*.

Soil fertility classes contrasted	Ratio±SE	z-ratio	p-value
meadow/Fertile	0.153 ± 0.047	-6.086	<.0001
meadow/Poor	0.309 ± 0.098	-3.717	0.0006
Fertile/Poor	2.026 ± 0.397	3.604	0.0009

* AICc=1572.443, $R^2_{conditional}$=0.879, $R^2_{marginal}$=0.529, ICC=0.743.

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