

## Article

# Enhanced Natural Regeneration Potential of Sessile Oak in Northern Hungary: Role of Artificially Increased Density of Insectivorous Birds

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**Abstract:** Both artificial and natural regeneration of oaks strongly depend on the quantity and quality of the acorn crop, which show high year-to-year variation. The volume of the acorn crop is influenced by many factors including biotic and abiotic effects. The quality (i.e., germination ability, nutrient reserves) of acorns can be decreased by carpophagous insect and fungal pathogen damage or by inadequate weather conditions. Defoliating insects (caterpillars, sawfly larva, etc.) can significantly decrease the acorn crop as well. The most important predators of the defoliators are insectivorous birds during their nesting period. However, in the oak forests of the northern Hungarian mountains, there is a shortage of natural nesting holes. The main aim of our study was to artificially increase the number of the available nesting holes by nest boxes and to maximize the number of breeding insectivorous birds and register the direct (Lepidoptera densities) and indirect (acorn crop quantity and quality) effects of their presence. We found only slight effects on Lepidoptera densities, so we failed to demonstrate a direct effect in the relatively low time frame of our study. But, we could show the indirect positive effect of increased predation on the health state of the acorn crop, resulting in higher seedling densities, which may improve the natural regeneration potential of sessile oak. This result supports the outstanding importance of natural nesting holes in broadleaved forests.

**Keywords:** Quercus; bird; caterpillar; insectivore; invertivore; nest box; acorn crop; seedling



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## 1. Introduction

Oak-dominated forest ecosystems are exceptionally important in the Northern Hemisphere both from an ecological and economic point of view, but in the last couple of decades, European oak forests are under increasing pressure due to climate change [1–5]. Both native and alien pathogens and insects are an ever-increasing burden [6–10]. It is widely agreed that the drought-related negative effect on oaks' health, as well the abundance of forest-defoliating insects, will increase as an indirect aftermath of climate change [11–13].

Both from economic and ecological (resistance/resilience) points of view, natural regeneration of oak forests—tending toward uneven aged and mixed stands—is preferred compared to artificial regeneration [14–16]. The lack or poor regeneration of oaks is a major problem in uneven-aged close-to-nature forestry [17].

The oak regeneration cycle can be divided in acorn production, germination and seedling survival. Artificial and natural oak regeneration depends on masting, which is hardly predictable. Both quantity and quality of acorn crop depend on a number of abiotic and biotic factors, including, among many others, weather conditions [18–21], stand density [22] and also herbivore impact [23]. Oak seed germination can fail for several reasons: abortion, herbivory by birds and mammals, insect attacks and fungal diseases, freezing, drying or excessive moisture [24]. In Hungary, there are 19 carpophagous insect species described: six weevils (Coleoptera, Curculionidae), four moths (Lepidoptera) and nine gall wasps (Hymenoptera) (Species list S1) [25]. One of the most common of the

several fungal diseases, *Ciboria batschiana* (Zopf) N.F.Buchw., can damage 80% of oak seeds in wet conditions [26]. In a dry environment, acorn viability is greatly reduced when internal moisture levels decrease below 36% [27]. Seedling survival is mostly influenced by the available light, interspecific competition, browsing and initial seedling density [28].

Among the biotic factors, defoliating insects have a major effect on the acorn crop. In European oak-dominated forests, the most abundant defoliators in the spring season are lepidopteran caterpillars [29]. The monthly numbers of native folivore species show a characteristic seasonal pattern in Hungary, peaking in April/May and dropping down in late May/early June [29,30]. Foliage consumption by herbivores reduces plant productivity, limits their growth and threatens their survival by reducing the amount of photosynthetic tissue [31,32]. Insect herbivory can also reduce plant fecundity both directly and indirectly. Direct effects are, for example, consumption of female flowers by herbivorous insects [23], while indirect effects result from lower flower numbers due to reduced shoot growth [33] or from increased acorn abortion rates [34].

Efficient control—if possible—of any damaging factors listed above may increase the success of the natural regeneration efforts. There is hardly any chance to influence weather conditions, but there are possibilities to reduce the negative effects of defoliating insects. Large scale chemical control should be excluded due to several reasons (high cost, undesired side effects, etc.). Luckily, pesticides are used less and less in European oak forests. Supporting and strengthening the natural regulatory processes are much more desirable. Enhancing natural regulation via top-down processes (i.e., predation) is extremely important [35].

Arthropods form the diet of most birds for at least part of their lifetime [36,37], and 60% of them depend on insect food sources [38]. In forests, an estimated 300 million tons of arthropod prey is consumed by insectivorous birds yearly (100 million tons of them in temperate and boreal forests) [38]. Most of the arthropods serve as prey particularly during the breeding season, when nestlings need protein-rich prey [39]. Caterpillars (lepidopteran larvae) and beetles (Coleoptera) are the most commonly consumed prey in temperate forests [40–42]. Easy digestibility and high protein content are the characteristics of the preferred diet of the nestlings, and this is fulfilled by the caterpillars [43]. The spring abundance peak of caterpillars overlaps with the nesting season of most insectivorous birds. Their diet in temperate habitats consists of 20%–90% caterpillars of abundant (therefore potential) pest species [30,42,44,45].

Processes that limit and regulate bird abundancies are thoroughly researched but still not fully elucidated [46,47]. Density-independent factors such as weather and food supply are not related to population size. At the same time, density-dependent processes are involved in the regulatory mechanisms. These mediate local interactions between individuals, their natural enemies, and their environment that cause demographic rates to increase or decrease when population density changes [48]. Density-dependent regulation implies that the variance of the population size is limited and that there is a mean population size or an equilibrium around which the population fluctuates [49]. If we are able to identify the limiting factors, then we will be able to artificially control the population size [50].

In Hungary there are 96 species of birds connected to forested habitats from the 424 native bird species [51,52]. More than half (50) of these forest-related bird species are insectivores [53], and half of them are hole breeders [54] (Table S1). In the mostly middle-aged and old Natura 2000 areas of the Northern part of Hungary, no holes on living trees were found in 98.15% of more than 60,000 sample points (500 m<sup>2</sup> circles), while no holes located in dead trees were found in 95.95% of the sample points, so very few nesting holes are available in these Hungarian forests [55]. These facts denote that there is strong competition for the nesting holes and the populations—therefore ecosystem services as well—are limited.

Our aim was to maximize the density of the insectivore bird population by experimentally eliminating the nesting hole shortage to answer the following questions:

1. Is there a direct effect of increased bird population on Lepidoptera populations?

2. Is there an indirect effect of increased bird population on acorn crop and oak regeneration potential?

We found slight direct effects of insectivorous birds on herbivore assemblages in three years, but we proved positive indirect effects on natural oak regeneration potential.

## 2. Materials and Methods

### 2.1. Study Site

Our study site was a 53–59-year-old coppice forest dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) located in the northern part of Hungary, in the Mátra mountains (47°51′02.9″ N, 19°55′12.9″ E) (Figure 1). When we selected the area, we paid particular attention to ensure that there was a very low number (less than 1 hectare<sup>-1</sup>) of natural holes in the forest. We established a sample plot of 5 hectares in 2018, where we intended to maximize the bird population by placement of 10 nest boxes per hectare, 53 in total (Figure 1). We used the most general, type B nest boxes (hole diameter 3.4 cm, base area 12.5 cm × 12.5 cm, height 25 cm), placed on tree branches at a height of 2–6 m. At the same time, we designated a control site that is 100 m apart from the sample site (Figure 1). The hole breeder species that are present at the sample site have lower moving range during feeding the nestlings than the distance between the sample and control sites (Table S2) [56–59].

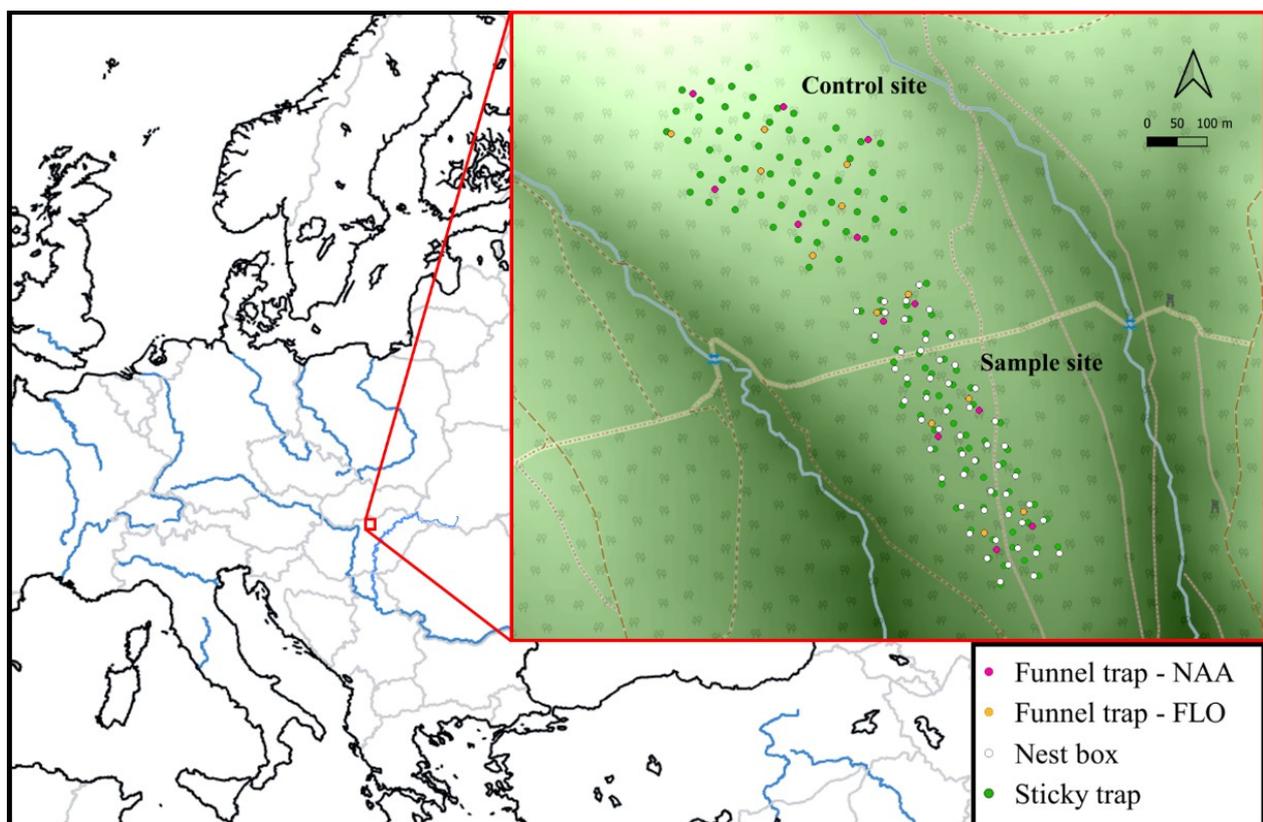


Figure 1. Map of the study site.

### 2.2. Data Collection

We collected the following nesting data from 2018 to 2022: species, nest with eggs, successful nests, egg number, hatched chicks, fledged chicks. We estimated caterpillar consumption using the literature data (Table S3) [60–64]. In our calculations, we considered the number of visits per hour, the length of the day, the length of breeding and the percentage of visits, when caterpillars are brought to the nestlings. The calculations were based on the number of successful nests. We performed a theoretical calculation of the caterpillar

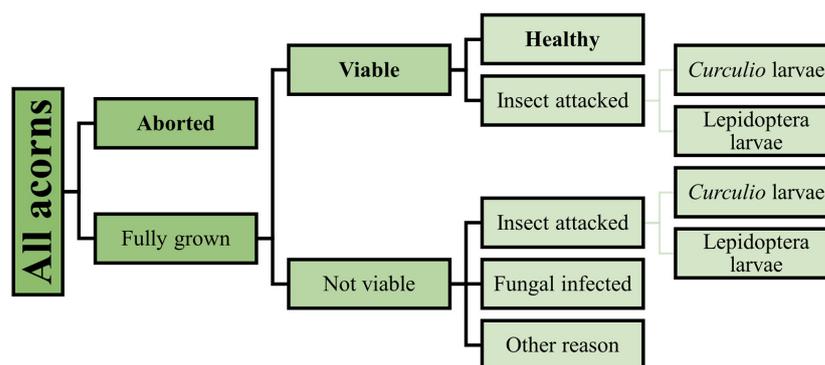
abundance at the sample site and what percentage of it could potentially be consumed by the birds nesting in the artificial nest boxes (Table S4) [65].

To evaluate the direct effects of the birds' predation, we used sticky belt traps on tree stems without bait to monitor the geometrid (Lepidoptera, Geometridae) moth population changes and baited funnel traps (Csalomon<sup>®</sup>, Budapest, Hungary) to monitor the noctuid (Lepidoptera, Noctuoidea) moth population changes. Data were collected from November to mid-April in 2019–2022. In both sample and control sites, 60 sticky traps were installed on tree trunks at breast height (Figures 1 and 2). The strips were 15 cm wide and sprayed with non-drying glue for insect traps (Fytofarm Chemstop Ecofix) (Figure 2). In order to eliminate the differences between tree trunk circumferences, the results were displayed in the number of individuals per one meter of trap length per day. The funnel traps were baited with fermenting, alcoholic fragrance (isoamyl alcohol, acetic acid, and red wine—NAA) and floral scent (phenylacetaldehyde, benzyl acetate, (E)-anethole and eugenol—FLO) (Figure 2). The baits were produced by Csalomon<sup>®</sup>. We placed 6 traps containing NAA and 6 traps containing FLO both at the control and sample sites (Figure 1). All Lepidoptera caught by the traps were identified to the species level. The flight of both winter and spring active moths has a unimodal distribution, and it starts with the arrival of foggy weather in winter and with warmer temperatures in spring. This allowed us to expect the flight intensity, and, according to that, all traps were checked and emptied every 2–7 days.



**Figure 2.** The installed sticky belt trap (left) and funnel trap (right).

To answer the question of whether increased bird abundance has an indirect effect on acorn crop, we sampled both the sample and control areas from September to the end of October in 2019–2021 and collected acorns from 75 fixed 1 m<sup>2</sup> quadrats to evaluate the quantity and quality of the acorn crop (Figure 3). All collected acorns were cut in half to check the condition of the cotyledons, radicle and epicotyl. If we found damage, we identified the carpophagous species or the pathogen. When radicle and epicotyl was intact, the acorn was declared viable. To calculate the natural regenerating capability of the forest, we counted the number of oak seedlings in 300 1 m<sup>2</sup> quadrats at both sites in the spring of 2021.



**Figure 3.** Health state categories of acorns. The categories written in bold were included in the model we used.

### 2.3. Data Analysis

We analyzed separately the two trap types and the differently baited funnel traps due to the barely overlapping species catch. In this analysis, the first season was November 2019–April 2020, the second was November 2020–April 2021 and the third season was November 2021–April 2022, and every season was divided into winter (November–January) and spring (February–April) as there are two moth guilds, the winter and spring active. This was labeled as subseason in the models we used. We also analyzed the data of the acorn crop and seedling counting separately.

We used Generalized Linear Mixed Model (GLMM) [66,67] for all calculations. Log-normal distribution fitted to all of our data best on the quantile-to-quantile plot. All calculations were made in R (version 4.1.1) [68]. For GLMM calculations, we used *car* [69], *MASS* [70], *lme4* [66] and *nlme* [71] packages.

#### 2.3.1. Sticky Belt Trap

We used generalized linear mixed model fit by maximum likelihood (Laplace’s approximation) [72]. In the model parameters, we set the family to Gaussian (log) and nAGQ to 1. The dependent variable was the number of geometrid moths (Geometridae) per meter per day, since this type of trap mostly caught this group. The fixed effects were the site (levels: sample, control), the season (levels: first, second, third), the subseason (levels: winter, spring) and the number of fledged chicks before the given season. Interactions were used to show the effect of fixed effects. The random effects included the site and the season. The model was not overdispersed (chisq = 4431.4, ratio = 0.822, residual df = 5391.0,  $p = 1.000$ ).

#### 2.3.2. Funnel Trap Baited with FLO

We used generalized linear mixed model fit by maximum likelihood (Laplace’s approximation) [72]. In the model parameters, we set the family to Gaussian (log) and nAGQ to 1. With this bait, we caught almost no individuals in the winter ( $n = 20$ ), so it was excluded from the analysis. In the model, the dependent variable was the number of noctuid moths (Noctuoidea) per trap per day, since this type of trap mostly caught this group. The fixed effects were the site (levels: sample, control), the season (levels: first, second, third) and the number of fledged chicks before the given season. Interactions were used to show the effect of fixed effects. The random effects included the site and the season. The model was overdispersed (chisq = 36,687.4, ratio = 103.930, residual df = 353.0,  $p = 0.000$ ), so we included the trap ID in the random effects to eliminate overdispersion.

#### 2.3.3. Funnel Trap Baited with NAA

We used generalized linear mixed model fit by maximum likelihood (Laplace’s approximation) [72]. In the model parameters, we set the family to Gaussian (log) and nAGQ to 1. In the model, the dependent variable was the number of noctuid moths (Noctuoidea)

per trap per day, since this type of trap mostly caught this group. The fixed effects were the site (levels: sample, control), the season (levels: first, second, third), the subseason (levels: winter, spring) and the number of fledged chicks before the given season. Interactions were used to show the effect of fixed effects. The random effects included the site and the season. The model was overdispersed ( $\text{chisq} = 132,074.6$ ,  $\text{ratio} = 235.008$ ,  $\text{residual df} = 562.0$ ,  $p = 0.000$ ), so we included the trap ID in the random effects to eliminate overdispersion.

#### 2.3.4. Acorn Crop

We used generalized linear mixed model fit by maximum likelihood (Laplace's approximation) [72]. In the model parameters, we set the family to Gaussian (log) and nAGQ to 1. In the model, the dependent variable was the number of acorns per  $\text{m}^2$ . The fixed effects were the site (levels: sample, control), health state (levels: all acorns, aborted, healthy, viable) and the number of fledged chicks before the given season. Interactions were used to show the effect of fixed effects. The random effects included the site and the year of collection. The model was overdispersed ( $\text{chisq} = 6,460,232.3$ ,  $\text{ratio} = 3603.030$ ,  $\text{residual df} = 1763.0$ ,  $p = 0.000$ ), so we included the quadrat ID in the random effects to eliminate overdispersion.

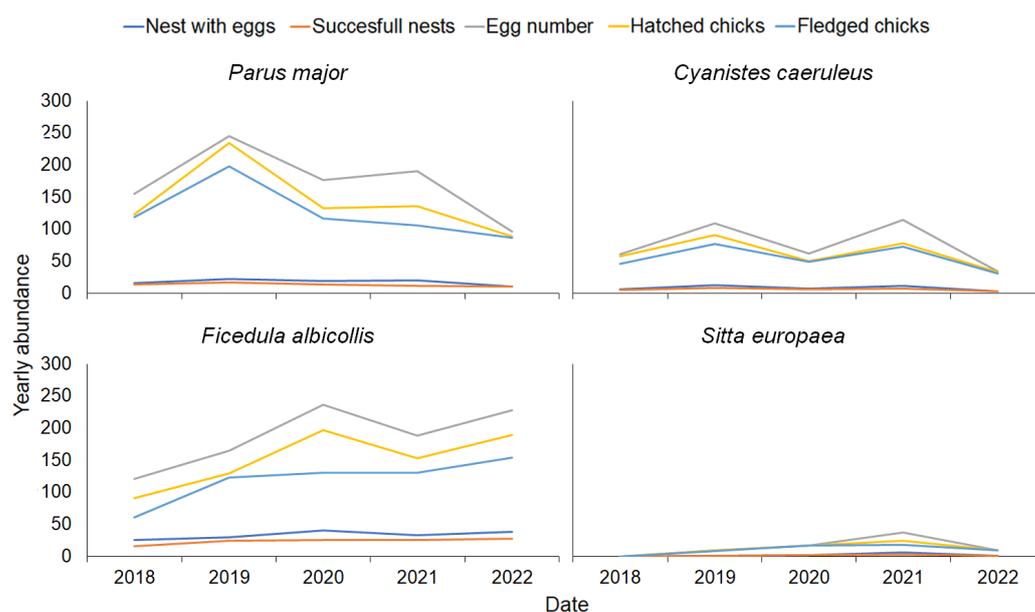
#### 2.3.5. Seedling Counting

We used the Penalized Quasi Likelihood (PQL) method [73]. In the model parameters, we set the family to Gaussian (log). The dependent variable was the number of seedlings per  $\text{m}^2$ . The fixed effect was the site (levels: sample, control), and the random effect was the quadrat ID. For multiple comparison of means, we used Tukey's test.

### 3. Results

#### 3.1. Bird Abundance Data and Estimated Caterpillar Consumptionnesting Data

During 2018–2022, there were 306 nesting attempts, of which 224 (73.2%) were successful. As a result, 1553 (68.9%) chicks fledged from the 2255 eggs laid. In total, four species occupied the 53 nest boxes (Figures 4 and 5, Table 1). In the first years (2018–2019), great tit (*Parus major* L., 1758) was the most abundant, while in the last years, collared flycatcher (*Ficedula albicollis* (Temminck, 1815)) became the most common. The blue tit (*Cyanistes caeruleus* L., 1758) constantly had a moderate abundance, and Eurasian nuthatch (*Sitta europaea* L., 1758) was a sporadic nester (Figure 4, Table 1).



**Figure 4.** Nesting statistics of the four species present at our study site.



**Figure 5.** The four species occupied the nest boxes. Top left: Great tit (*Parus major* L., 1758) with a noctuid larva prey. Top right: Blue tit (*Cyanistes caeruleus* L., 1758). Bottom left: Eurasian nuthatch (*Sitta europaea* L., 1758). Bottom right: collared flycatcher (*Ficedula albicollis* (Temminck, 1815)) on its nest.

**Table 1.** Nesting statistics of the species present at our study site in nest boxes and the estimated caterpillar consumption. The estimated caterpillar consumption is calculated for the successful nests. Caterpillar consumption per brood is calculated by using bibliographic data (Table S3).

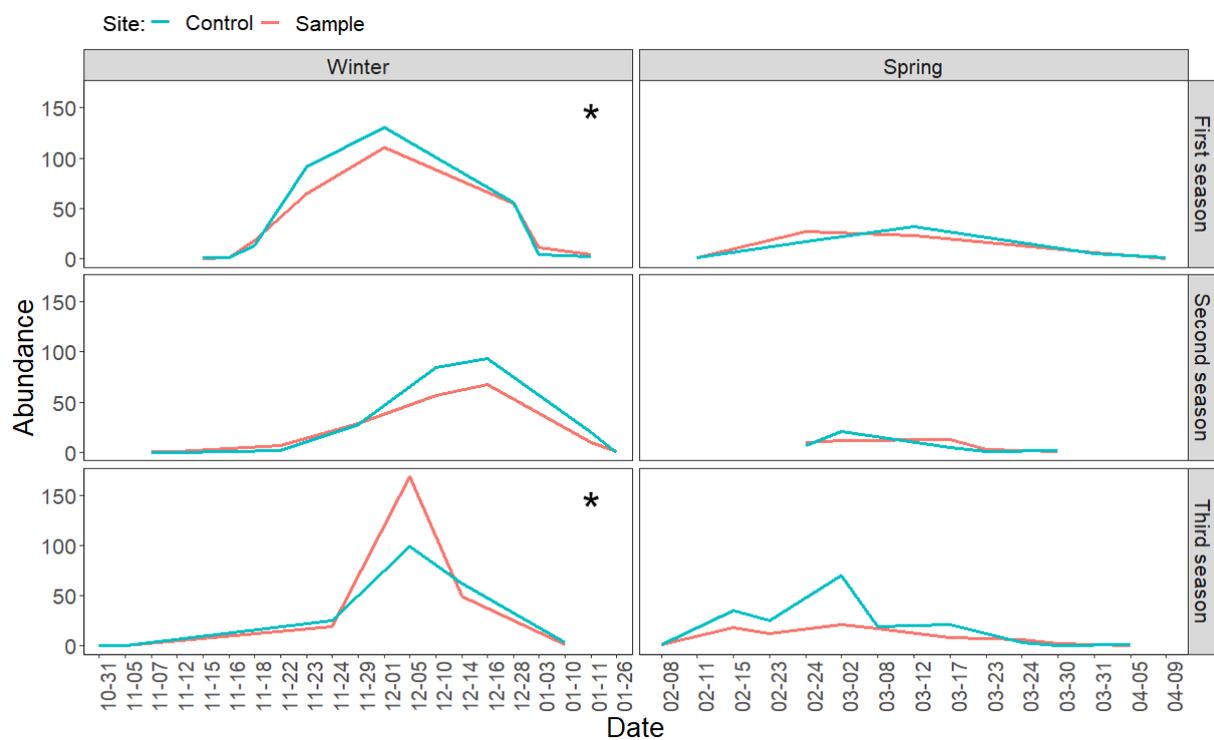
Species	Year	Nest With Eggs	Successful Nests	Egg Number	Hatched Chicks	Fledged Chicks	Estimated Caterpillar Consumption (Individuals)
<i>Cyanistes caeruleus</i> L., 1758	2018	6	5	61	58	46	41,795
	2019	13	8	109	91	77	66,872
	2020	7	6	62	50	49	50,154
	2021	12	7	114	78	73	58,513
	2022	3	3	34	33	31	25,077
<i>Ficedula albicollis</i> (Temminck, 1815)	2018	25	16	121	91	61	91,872
	2019	30	24	165	129	123	137,808
	2020	41	26	237	197	130	149,292
	2021	33	26	188	153	130	149,292
	2022	38	28	228	189	154	160,776
<i>Parus major</i> L., 1758	2018	16	14	155	123	119	49,448
	2019	22	17	245	235	198	60,044
	2020	19	14	177	133	117	49,448
	2021	20	12	191	136	106	42,384
	2022	11	11	96	89	87	38,852
<i>Sitta europaea</i> L., 1758	2018	0	0	0	0	0	0
	2019	1	1	9	9	8	3059
	2020	2	2	17	17	17	6118
	2021	6	3	37	24	18	9177
	2022	1	1	9	9	9	3059
All species	2018	47	35	337	272	226	183,115
	2019	66	50	528	464	406	267,783
	2020	69	48	493	397	313	255,012
	2021	71	48	530	391	327	259,366
	2022	53	43	367	320	281	227,764

We estimated the amount of consumed caterpillars per brood according to the literature data (Table S3). The estimated that caterpillar consumption was on a continuous level over

the years (Table 1). The collared flycatcher consumed the most caterpillars at our sample site, followed by great tit and blue tit (Table 1). The consumed caterpillars can account for 10%–30% of the amount available in the forest (Table S4).

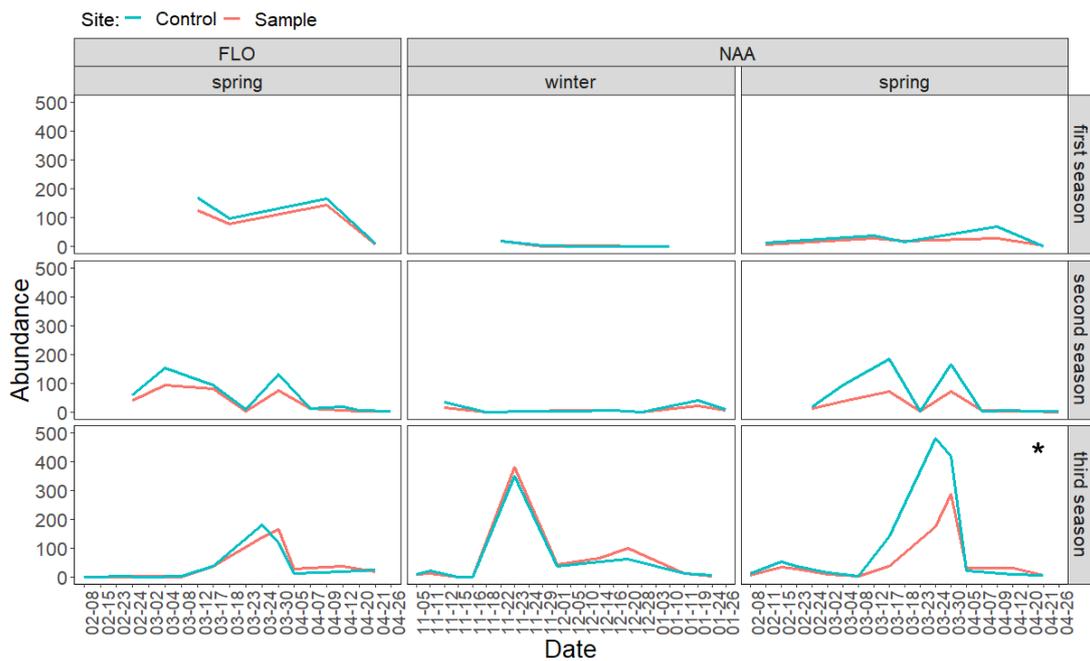
### 3.2. Direct Effects of Increased Bird Abundancies on Lepidoptera Populations

We caught 10,159 individuals with the sticky belt trap during the three study seasons. Most of the catches were Geometridae (ncontrol = 5273; nsample = 3741). We caught lower numbers of Microlepidoptera (ncontrol = 484; nsample = 558) and Noctuidae (ncontrol = 58; nsample = 44) and only 1 *Poecilocampa populi* L. 1758 (Lasiocampidae) at the sample site; the three groups accounted for a total of 11.27% of the catches. Most of the time, sample catches were lower than control catches (Figure 6). We found no significant differences in geometrid moth catchment of the sticky belt trap, only the catchment of winters of the first and third season was close to significance, but in a different direction (Figure 6, Table S5).



**Figure 6.** Geometrid moth catches of sticky belt traps during the three study seasons. \* denotes  $0.1 > p > 0.05$  for the period (subseason).

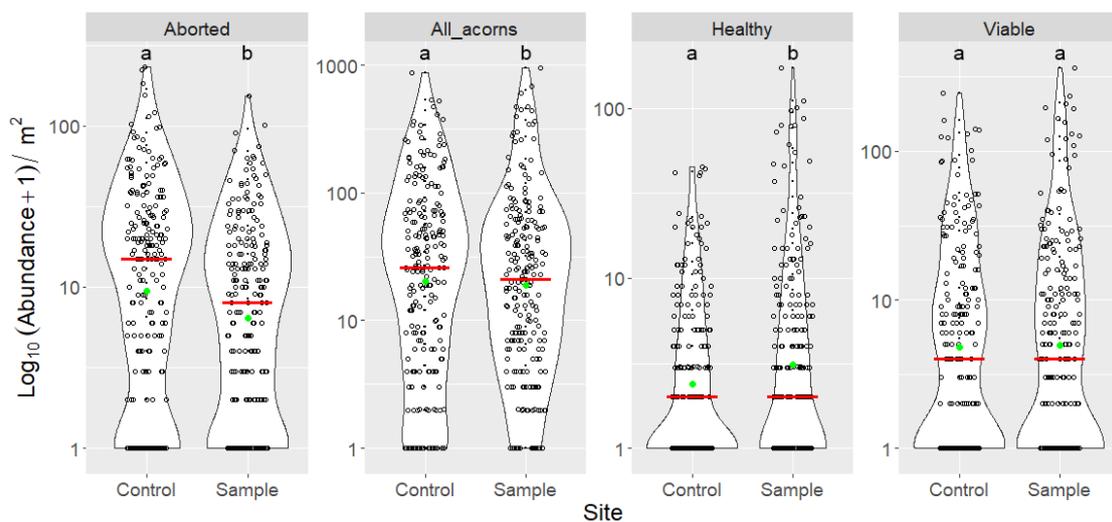
We caught 11,492 individuals with the baited funnel traps (Table S6). Noctuoidea was the most abundant group caught (NAA: ncontrol = 4036; nsample = 3948; FLO: ncontrol = 1364; nsample = 1130) (Table S6). All the other groups (Geometridae, Thyatiridae, Sphingidae, Drepanidae, Diurna and Microlepidoptera) made up 7.05% of the catches (Table S6). Most of the time, control and sample catches run together, or control catches are slightly higher. The only period when control catches were significantly higher than sample catches was the spring of the third season in the funnel trap baited with NAA (Figure 7, Tables S7 and S8).



**Figure 7.** Noctuid moth catches of funnel traps during the three study seasons. \* denotes  $p < 0.05$  for the period (subseason).

### 3.3. Indirect Effects of Increased Bird Abundancies on Acorn Crop and Regeneration Potential

A total of 28,556 acorns were collected: 14,992 acorns from the control site and significantly less, 13,564, acorns from the sample site (Figure 8, Tables 2 and S9). From these, 8186 (28.7%) acorns were aborted and 20,370 (71.3%) fully grown. We found significantly lower aborted acorn densities at the sample site than at the control site (Figure 8, Tables 2 and S9). We also found significantly higher healthy acorn densities at the sample site compared to the control site, but we found no differences in viable acorn densities (Figure 8, Tables 2 and S9).

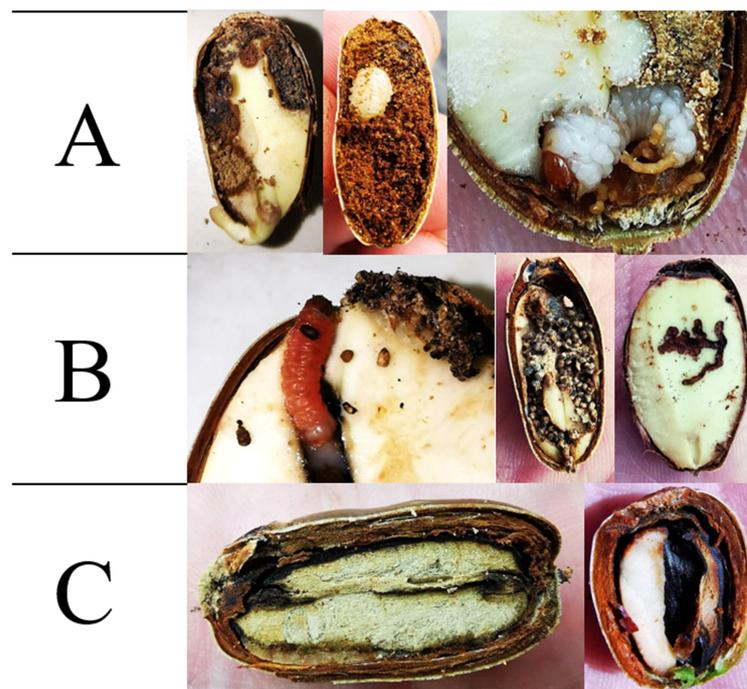


**Figure 8.** Violin plot of the  $\text{Log}_{10}$  number of acorns of different health state categories per  $\text{m}^2$  according to the site. The violin plot is a rotated, smoothed probability density distribution that describes the underlying shape of the data. Red line: median, green dot: arithmetical mean. Different lower-case letters refer to significant differences.

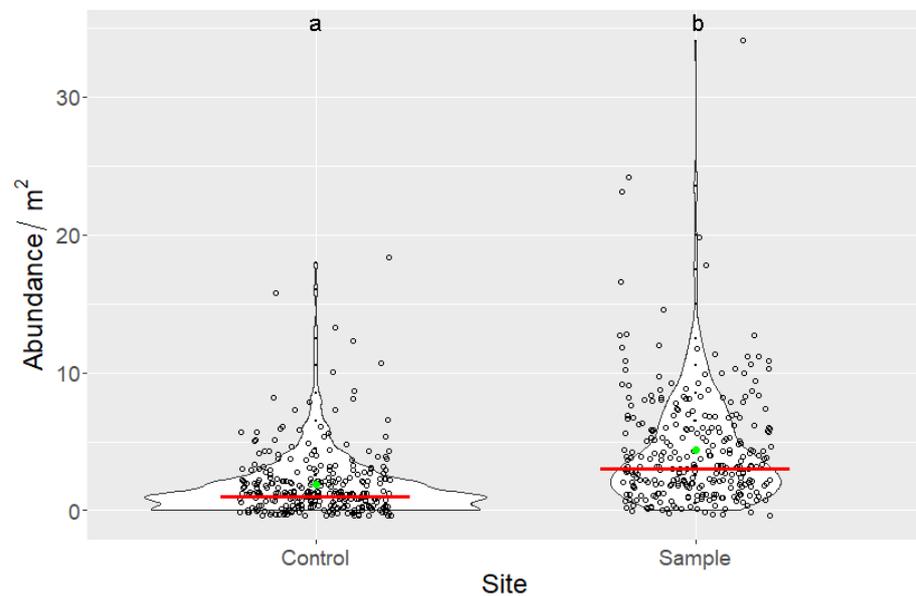
**Table 2.** Summary statistics of acorn crop. The categories written in bold were included in the model we used.

Site	Categories	<i>n</i>	Min	Max	Mean	Median	SD	Sum
Control	<b>Aborted</b>	225	0	231	22.880	14	33.619	5148
	<b>All acorns</b>	225	0	868	66.631	25	109.628	14,992
	Curculio attacked	225	0	367	23.227	6	45.869	5226
	Fully grown	225	0	637	43.751	12	80.933	9844
	Fungal infection	225	0	65	5.080	1	9.359	1143
	<b>Healthy</b>	225	0	44	3.698	1	7.502	832
	Insect attacked	225	0	532	34.640	9	66.616	7794
	Lepidoptera attacked	225	0	165	11.413	4	21.578	2568
	Other reason	225	0	9	0.333	0	1.039	75
	<b>Viable</b>	225	0	247	14.711	3	30.978	3310
Sample	<b>Aborted</b>	225	0	151	13.502	7	19.531	3038
	<b>All acorns</b>	225	0	945	60.284	19	119.636	13,564
	Curculio attacked	225	0	330	21.093	5	46.665	4746
	Fully grown	225	0	855	46.782	12	106.319	10,526
	Fungal infection	225	0	147	6.320	1	16.461	1422
	<b>Healthy</b>	225	0	171	8.329	1	21.043	1874
	Insect attacked	225	0	536	31.929	10	70.143	7184
	Lepidoptera attacked	225	0	206	10.836	3	24.201	2438
	Other reason	225	0	5	0.204	0	0.592	46
	<b>Viable</b>	225	0	362	18.151	3	43.720	4084

We identified carpophagous groups like larvae of *Curculio* spp. (control = 35.0%; sample = 35.0% of all acorns) and lepidopteran larvae (control = 17.2%; sample = 18.0% of all acorns) (Figure 9, Table 2). We found fungal infections (control = 7.7%; sample = 10.5% of all acorns) (Figure 9) and other reasons such as consumption by rodents (control = 0.5%; sample = 0.3% of all acorns) in lower numbers (Table 2). None of the fungal attacked acorns were viable, while the 31.7% (control) and 30.9% (sample) of the insect attacked acorns were viable.

**Figure 9.** Attacked or infected acorns. (A): *Curculio* attacked acorns, (B): Lepidoptera attacked acorns, (C): fungal infections.

A total of 1877 seedlings were counted in 600 quadrats, and we found significantly denser stock at the sample site than at the control site (Figures 10 and 11, Tables 3 and S10).



**Figure 10.** Violin plot of the  $\text{Log}_{10}$  number of seedlings per  $\text{m}^2$  according to the site. The violin plot is a rotated, smoothed probability density distribution that describes the underlying shape of the data. Red line: median, green dot: arithmetical mean. Different lower-case letters refer to significant differences.



**Figure 11.** Sessile oak (*Quercus petraea*) seedlings at our study site.

**Table 3.** Summary statistics of the seedling counts.

Site	<i>n</i>	Min	Max	Mean	Median	SD	Sum
Control	300	0	18	1.873	1	2.424	562
Sample	300	0	34	4.383	3	4.131	1315

#### 4. Discussion

We were able to artificially increase the insectivorous bird population at the sample site. After all, almost all nest boxes were occupied every year. This is a clear indication that the bird population is strongly limited by lack or shortage of suitable nesting holes. However, we could identify only a slight direct effect in short term results, which shows unclear trends. At the same time, accumulated indirect effects resulted in better quality of the acorn crop and significantly enhanced regeneration potential of the forest. At the end of autumn, when we checked the health state of the acorns, we found about the same amount of viable acorns, but the proportion of healthy acorns within the viable acorns increased greatly at the sample area. By the spring, insect-attacked viable acorns most probably became not viable, resulting in significantly higher seedling density.

An increased insectivorous bird population resulted in lower caterpillar density and body mass and in less damage on Pyrenean oak leaves (*Quercus pyrenaica* Willd.) after 10 years [74]. This result points out that a slightly longer period of presence of increased predation is likely enough to show significant direct effect. Experiments using predator exclosures showed similar results [39,75]. The absence of insectivore vertebrates increases the arthropod population by 69% [76]. Placing nest boxes in much more human modified habitats, such as vineyards and orchards have already been proved to lower the herbivore abundancies in a given year [77,78]. The predation rates on artificial caterpillar prey are positively correlated with the bird densities in forested habitats [65].

However, some of these arthropods are predators. According to the mesopredator release hypothesis, the number and predatory activity of small predators freed from their own predators and competitors will increase [79]. However, for this, it is necessary that there are sufficient habitats for these organisms in the forest, primarily dead wood in a suitable quantity and condition [80–82]. At our sampling site, there were low amounts of dead wood; thus, the absence of insectivorous birds can only slightly increase the predatory arthropod abundancies in the control area. An increased arthropod population alongside its negative effect can have positive effects. Insect frass is rich in nitrogen and nutrients, which are easy to assimilate by plants [83]. This positive effect was shown in the case of the eastern tent caterpillar (*Malacosoma americana* (F., 1793)) and white-marked tussock moth (*Orgyia leucostigma* J.E.Smith, 1797) on red oak (*Quercus rubra* L.) [84] or the gypsy moth (*Lymantria dispar* L., 1758) and the forest tent caterpillar (*Malacosoma disstria* Hübner) on trembling aspen (*Populus tremuloides* Michx.) [85]. Increased nitrogen levels in the soil also can cause a better defense mechanism by accumulation of amino acids and proteins, as it was shown on Scots pine (*Pinus sylvestris*) after defoliation of nun moth (*Lymantria monachal* L., 1758) [86]. Moreover, arthropod frass contains microorganisms that are able to promote plant growth, increase their tolerance to abiotic stresses, and decrease the damaging effect of biotic stresses [87]. As the insectivore population is not significantly lower at the sample site than at the control site, this positive effect is still present.

The amount of caterpillars in oak-dominated forests in Hungary that are suitable food for nestlings is increasing [88]. There are two main reasons for this. First, there is widespread agreement that the impacts of insects damaging forests will increase as an indirect effect of climate change [6,10,12]. The other reason is the expected change in the status of the gypsy moth, the major defoliator in broadleaved forests of East-Central Europe [89]. It is forecasted that the gypsy moth outbreaks in Central Europe will be less frequent, less intensive and the size of the damaged area will decrease [90] due to the presence and impact of the *Entomophaga maimaiga* Humber, Shimazu & R.S.Soper, a strongly host-specific pathogen, suppressing the gypsy moth populations [91–93]. Its densely hairy larvae—usually less eaten by birds—will probably be at least partly replaced by smooth and less hairy larvae of other defoliators (most of the tortricids, geometrids and noctuids). This means that with the increased amount of suitable food, the positive effect and importance of predation of insectivorous birds can be higher than it was in the past.

Our results evidently have some limiting factors. We did not repeat the study in several locations because of the shortage of funding and capacity. Otherwise, Hungarian

forests are generally fragmented in terms of forest age and species composition. It is difficult to find a large enough continuous and homogeneous sampling site that is close enough to our department for daily control and meets all other criteria. On the other hand, our results are short-term, in terms of ecological mechanisms. Finally, the hole-nesting insectivorous birds are not the only species that are controlling the folivores. There are several other insectivore and parasitoid species that have the same, if not greater, effect. Long-term research with continuously high effort is extremely expensive and rare. As, regularly, only a small percentage of the total acorn crop can be considered as healthy under natural conditions [25], small changes can result in big differences in the success of natural regeneration. Bird predation on carpophagous insects can improve the quality of the acorn crop. Although there is almost no information about fledgling dispersion in the first months, great tit dispersal from birth to first breeding site ranges between 113 and 718 m (mean values) [94,95], which suggests that they feed in the surroundings of their birth site. Consuming acorn weevils decreases the number of egg-laying holes made by weevils, which also lowers the probability of fungal infections of acorns [96].

Natural regeneration of sessile oak forests has several positive effects. First, it preserves natural genetic diversity [97]. Second, it allows natural selection from the large abundance of seedlings and promotes the development of a natural and undisturbed root system, which leads to better stand stability [98]. However, there are factors that hinder natural regeneration, such as advanced regeneration of shade-tolerant species, scarcity of mast acorn crops, presence of competition from ground vegetation and the costly requirement to protect acorns and seedlings against browsing [99,100]. The percentage of acorns attacked by insects was similar to previous Hungarian results (52.0%–52.7% vs. 20%–65%), while the amount of viable insect-attacked oak seeds was lower than the literature data (30.9%–31.7% vs. 39%–64%) [96]. The density of seedlings was not higher or lower than the range given in the European literature (0.15–23 individuals per m<sup>2</sup>) [28].

## 5. Conclusions

Our results suggest that short-time natural level predation can indirectly lower the abortion rates and increase the quality of a viable acorn crop resulting in higher density of seedlings, which leads to a better natural regeneration capability [28]. We think that the most important role of insectivorous birds is not necessarily the consumption of the caterpillar population of a given year, particularly not in outbreak periods. Their impact is more important in years when the caterpillar density is lower (negative density dependence), since the proportion of the caterpillars consumed is higher than in outbreak years [49] and so they may elongate the time between outbreaks. These results again underline the outstanding importance of saving and even increasing the number of natural nesting holes in the broadleaved forests.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14081548/s1>. Species list S1: Carpophagous insects described from Hungary; Table S1: Forest habitat connected species in Hungary their foraging, nesting and population information; Table S2: Moving range, territory and foraging flight distance of hole breeder insectivorous birds; Table S3: Estimated caterpillar consumption of bird species; Table S4: Estimated number of caterpillars at sample site and the proportion of consumed caterpillars at each study year; Table S5: Results of statistics of data collected by sticky belt trap; Table S6: The catches of the lepidopteran groups with different baited funnel traps at the sample and control sites; Table S7: Results of statistics of data collected by funnel traps baited with FLO; Table S8: Results of statistics of data collected by funnel traps baited with NAA; Table S9: Results of statistics of acorn crop data; Table S10: Results of statistics of data collected by seedling counting.

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