

Article

No Long-Term Decrease in Caterpillar Availability for Invertivorous Birds in Deciduous Forests in Hungary

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Abstract: Numerous recent studies report an alarming decrease in diversity, biomass, or abundance of arthropods in various habitats. Given that they are important food for other organisms, the ecological consequences of such a decline could be severe. We used data from the Hungarian Forestry Light Trap Network to examine whether the spring caterpillar biomass showed any long term (23–58 years) declining trend in oak-dominated forests. Light trap data for 43 selected macrolepidopteran species (suitable bird food in the larval stage) from six different locations were used for the estimation of the total available caterpillar biomass. Time series analyses showed strong year-to-year fluctuations, and over all locations and time windows there was an increasing rather than decreasing trend. The increase found at some locations may suggest increasing herbivore pressure and negative impacts on forest health. We conclude that foliage-feeding macrolepidopteran species with spring-developing larvae did not show a drastic decrease in recent decades, and food availability in the long term will not negatively influence the breeding success of birds in such forests.

Keywords: broadleaved forest; arthropod abundance; biomass; insectivore; long term trends; light trap; temperate



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1. Introduction

Several recent articles show or claim a dramatic decrease in arthropod diversity and biomass [1–3]. A serious decline in flying insect biomass is reported over 27 years in 63 nature protection areas in Germany [1]. These authors found this decline regardless of habitat type, therefore changes in weather, land use, or habitat characteristics cannot explain this overall pattern. Similar declines were found in the Netherlands [2]. Long-term species loss and homogenisation of moth communities were also demonstrated in Hungary [3]. Significant changes in land use are thought to be the main cause.

The main reasons of worldwide decline in entomofauna are believed to include: (i) habitat loss, intensive agriculture, urbanisation, (ii) pollution, (iii) biotic factors including pathogens and introduced pests, (iv) climate change [4].

The evidence for this is fragmented and uneven, mostly because suitable long-term data are scarce, making the existing long term data sets extremely valuable and informative [5]. Some of these datasets emerged from monitoring species of economic importance, many of which are attracted to light. The standardised light traps operating at the same place for a long enough period are excellent potential tools for following the population fluctuations and long term abundance trends of insect species attracted to artificial light [6–10].

The ecological consequences of arthropod decline would be profound because arthropods play many important and irreplaceable roles in ecosystem functioning [11–13]. One

of their major contributions is providing food for various groups of invertivorous organisms. Most birds feed on arthropods for at least part of their lifetime [14,15] and 60% of them depend on insect food sources [16]. Invertivorous birds in forests consume an estimated 300 million tons of arthropod prey yearly (one third of this in temperate and boreal forests [17], especially during the breeding season, when nestlings need protein-rich prey [17]). The most commonly consumed prey in temperate forests and agricultural habitats are lepidopteran caterpillars and beetles (Coleoptera) [18–20]. Caterpillars are a preferred diet because of their easy digestibility and high protein content [21]. The spring abundance peak of caterpillars overlaps with the nesting season of most invertivorous birds. During their breeding season, 20–90% of the nestling diet in temperate habitats are caterpillars of pest species [20,22–24]. The availability of caterpillars has a major influence on breeding success of both great—(*Parus major* L., 1758) and blue tits (*Cyanistes caeruleus* L., 1758) [21,25].

Consequently, any long term negative trend in the abundance of this important food source (particularly in the breeding season) may have a major effect on the breeding success of invertivorous birds [26]. To assess whether decreases in light-trapped moths has led to reduced caterpillar biomass in the studied Hungarian forests, we used a two-step process. First, we developed a method of calculating species-specific caterpillar biomass values for the relevant species. Subsequently, we analysed the fluctuations of caterpillar biomass, using long-term (23–58 years) adult moth datasets collected within the Hungarian Forestry Light Trap Network. We hypothesised a decline in moths translated into reduced food base for spring-breeding forest birds.

Overall, we found increasing rather than decreasing trends in caterpillar biomass that indicated no food shortage for birds during the breeding season.

2. Materials and Methods

2.1. Estimating the Relative Abundances of the Selected Species

We used data from the Hungarian Forestry Light Trap Network run by the Hungarian Forest Research Institute since the early 1960s. The whole network had light traps at 64 sites (with shorter or longer operating periods), of which 23 are still operational. The traps of the network have a uniform design, incorporating high pressure mercury vapor lamps (Tungsram, HgLi 125W, product code: 505506, Budapest, Hungary), and are operated continuously between 1 March and the end of December (from sunset to sunrise on ca. 300 days every year). The traps are emptied daily, and the macrolepidopteran species are identified [9].

From the full dataset, we selected a subset conforming to the following conditions:

1. The trap was set in or near a broadleaved (mainly oak) forest stand.
2. Has been working for at least 20 years.
3. Has been operated continuously, with a max. one year “time gap”.
4. The last year in the time series had to be 2019.

There were 6 traps that fulfilled these conditions (Figure 1, Table 1). From these traps, we included data on 43 common and abundant folivorous macrolepidopteran species (3 Drepanidae, 18 Geometridae, 2 Lasiocampidae, 18 Noctuidae, 2 Notodontidae) (Table S1) that had the following characteristics:

1. The species was univoltine.
2. Its caterpillars fed on the foliage of woody plants (trees and shrubs).
3. Its caterpillars developed in spring or early summer (from April to June) overlapping with the breeding season of invertivorous birds.
4. The caterpillars were neither densely hairy, nor contained poisonous chemicals, likely to be regularly consumed by invertivorous birds.
5. The species did not overwinter as adult.
6. The species was regularly caught in most years and places.

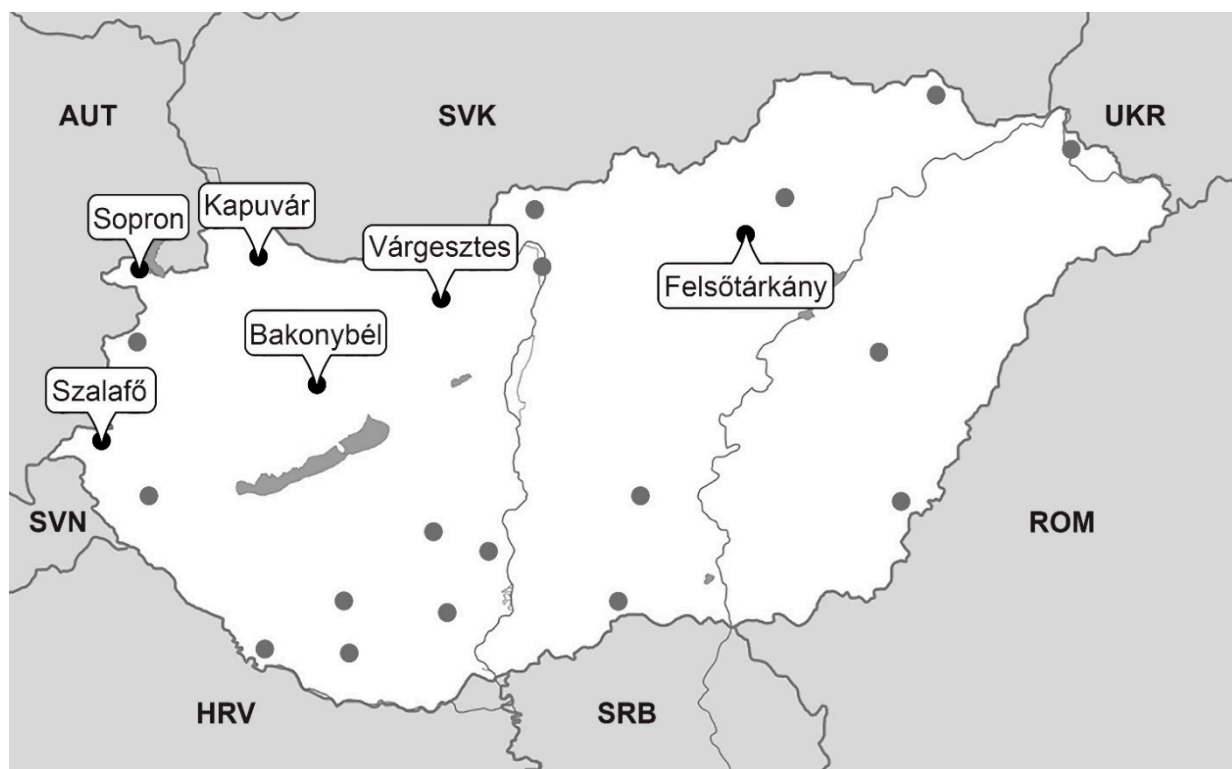


Figure 1. The locations of the light traps included our analysis (black dots and names of nearest settlements). Grey dots show the locations of working light traps not included in our current analysis.

Table 1. Location information, time period and numbers of Lepidoptera included in the analysis from the 6 light traps involved in the study, arranged from east to west by location.

Trap Location	Trap Coordinates	Altitude (m)	Forest Stands Around the Trap	Period	Length (Years)	Number of Individuals in Calculation
Felsőtárkány	47°58'51" N 20°26'03" E	238	Oak (<i>Quercus petraea</i> (Matt.) Liebl.) and hornbeam (<i>Carpinus betulus</i> L.) dominated mixed forests.	1962–2019	58	108,224
Várgesztes	47°28'18" N 18°23'54" E	286	Turkey oak (<i>Quercus cerris</i> DC.) and hornbeam (<i>C. betulus</i>) dominated mixed forests.	1963–2019	57	138,589
Bakonybél	47°15'04" N 17°45'41" E	390	Oak (<i>Quercus robur</i> L.) and hornbeam (<i>C. betulus</i>) dominated mixed forests.	1992–2019	28	59,051
Kapuvár	47°41'16" N 17°00'30" E	120	Oak (<i>Q. robur</i> and <i>Q. cerris</i>) dominated mixed broadleaved forests.	1993–2019	27	83,179
Sopron	47°39'51" N 16°33'14" E	375	Oak (<i>Q. petraea</i>) and beech (<i>Fagus sylvatica</i> L.) dominated mixed broadleaved forests.	1997–2019	23	41,036
Szalafő	46°51'19" N 16°22'33" E	264	Oak (<i>Q. robur</i>) and hornbeam (<i>C. betulus</i>) dominated mixed broadleaved forests.	1986–2019	34	40,403

The majority of these species were either polyphagous/oligophagous on broadleaved woody plants or monophagous on oak. There were two exceptions: *Ptilophora plumigera* ((Dennis and Schiffermüller) 1775) (Notodontidae) which feeds on *Acer* spp. (Sapindaceae) and *Achlya flavicornis* (L., 1758) (Drepanidae) which is a specialist of *Betula* spp. (Betulaceae)

Two species (*Bena bicolorana* (Fuessly, 1775) (Nolidae) and *Pseudoips prasinana* (L., 1758) (Noctuidae)) were excluded from this analysis due to earlier taxonomic/nomenclature confusion.

For species overwintering as eggs (e.g., *Operophtera brumata* (L., 1758) (Geometridae), *Erannis defoliaria* (Clerck, 1759) (Geometridae)), we considered the yearly catch as an indicator of the spring caterpillar biomass of the same year. For species overwintering as pupae (e.g., *Orthosia gothica* (L., 1758) (Noctuidae), *Alsophila aescularia* (Dennis and Schiffermüller, 1775) (Geometridae)) the subsequent year's catch data were used as indicators for a given year's spring caterpillar biomass. In other words, we used a one year lag in the analysis for these species.

2.2. Estimating the Caterpillar Body Mass

The average length (L, mm) of the fully grown caterpillar was taken from the literature [27,28]. Caterpillar diameters were measured on 1–3 digital images (photos taken with Canon DSLR cameras equipped with macro lenses) of fully grown larvae using Adobe Photoshop (Version: 21.0.2). The volume (V, mm³) of a single larva was estimated as the volume of a cylinder, based on the length and diameter. The resulting value was multiplied with the specific density of water (0.001 g/mm³) and used as a proxy for caterpillar biomass (Table S1).

2.3. Calculation of the Estimated Total Caterpillar Biomass Index

The yearly totals caught of each selected species by each trap were multiplied by the estimated larval biomass of the given species to obtain a caterpillar biomass index (CBI, g). The total of the species-specific CBIs provided the estimate of the available caterpillar biomass for the given site and year. The fluctuation of these CBIs were analysed further. Although the light trap catch data give indirect and imperfect estimations of the spring caterpillar biomass, significant positive correlations between light trap catches and caterpillar abundance (expressed as defoliation damage related to caterpillar abundance) are documented for several important oak defoliating Lepidoptera including *Lymantria dispar* (L., 1758) (Lymantriidae) [29], *Euproctis chrysorrhoea* (L., 1758) (Erebidae) [30], *Malacosoma neustria* (L., 1758) (Lasiocampidae) [31], spring feeding geometrids [32], and *O. brumata* [33]. Therefore, we conclude that light trap catches can give a good indirect estimation of the abundance of spring caterpillars and the long-term trend of moth abundance can be considered an indication of long-term trend in caterpillar biomass changes.

2.4. Statistical Analysis

We analysed the time series of each location separately because the light trap catches were not directly comparable due to their different surroundings and periods of operation. We used a simple linear regression model based on ordinary least squares method in R version 3.5.1. [34]. The response variable was CBI, while the explanatory variable was the year; the model validation was made considering the residuals. For further analysis for any trend, we used a locally weighted regression (LOESS) with $\alpha = 0.8$ [35]. With this method, we were able to detect a shifting point in the relative caterpillar biomass changes at one location (Várgesztes). Shifting point was determined as any change from decrease to increase or vice versa and if it was constant at least for 20 years. We set the significance level at $p < 0.05$. Due to the one year lag mentioned above, we had to leave out the last year (2019) from the trend analysis.

3. Results

Overall, we found no convincing evidence for long term declines in CBI. We found non-significant linear trends at four of the six locations; at the remaining site sites, the CBI showed significantly increasing trends.

3.1. Locations with Non-Significant Trends

We found non-significant trends at (from west to east): Szalafő, Sopron, Kapuvár, and Várgesztes.

The linear trend at Szalafő was increasing, but not significantly. According to LOESS results we could not apply any further analysis (Table 2, Figure 2). We found no significant trend at Sopron with a slight decrease in CBI (Table 2, Figure 2).

Table 2. Results of the trend analyses for six trap locations and analysis for different time windows in case of Várgesztes. Significant trends are given in bold.

Trap Location	Period Analysed	Equation	R^2	F-Statistic	DF	p -Value
Szalafő	1986–2018	$Y = 42.6X - 84280.4$	0.1102	3.591	29	0.0681
Sopron	1997–2018	$Y = -21.1X + 44024.5$	0.0131	0.266	20	0.6117
Kapuvár	1993–2018	$Y = 78.1X - 152889.2$	0.0342	0.814	23	0.3764
Várgesztes	1963–2018	$Y = -2.6X + 2565.4$	0.0001	0.042	53	0.8398
Várgesztes	1997–2018	$Y = 175.4X - 350478.0$	0.3257	9.659	20	0.0056
Bakonybél	1992–2018	$Y = 288.0X - 574272.9$	0.3199	9.877	21	0.0049
Felsőtárkány	1962–2018	$Y = 29.0X - 56333.8$	0.0994	5.738	52	0.0202

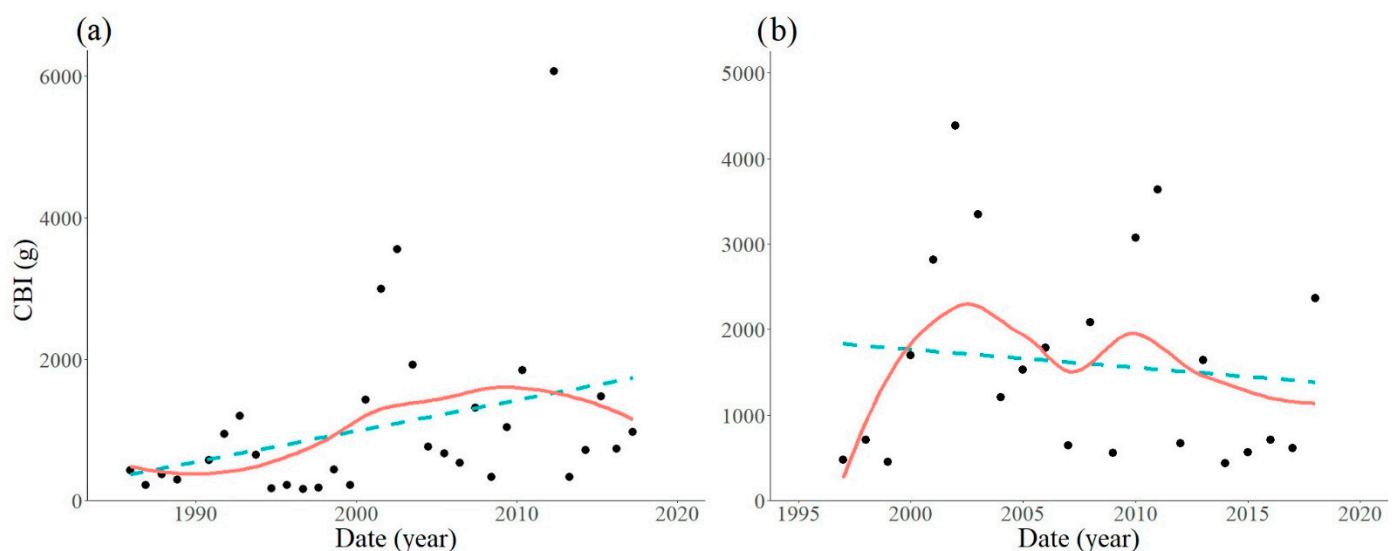


Figure 2. Yearly values and long term trends of the estimated spring caterpillar mass at Szalafő (a), and Sopron (b). (CBI, Caterpillar Biomass Index; blue dashed line, linear regression; red line, locally weighted regression with $\alpha = 0.8$).

In Kapuvár, we found a non-significant increasing trend, but the LOESS curve showed a cyclic change in CBI (Table 2, Figure 3). At Várgesztes, we found a non-significant decreasing trend, but the LOESS curve showed first a steep decrease, a shifting point in 1997, followed by a strong increase. A partial linear regression for the period of the last 23 years (1997–2018) indicated a significant increase ($p = 0.0056$) (Table 2, Figure 3).

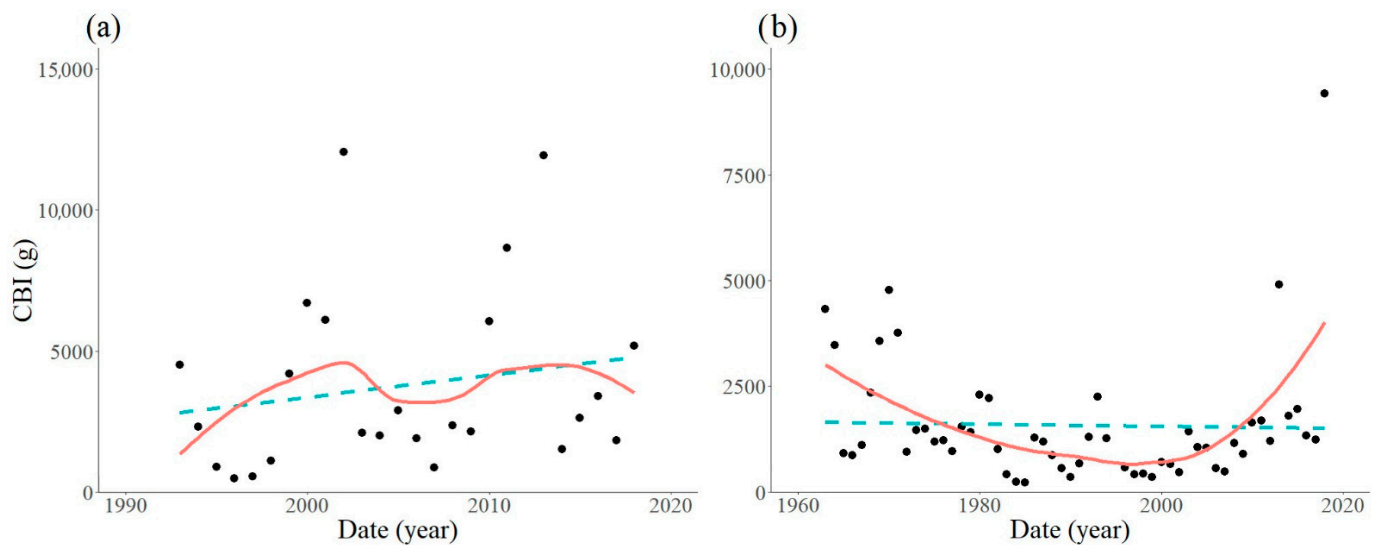


Figure 3. Yearly values and long term trends of the estimated spring caterpillar mass at Kapuvár (a), and Várgesztes (b). (CBI, Caterpillar Biomass Index; blue dashed line, linear regression; red line, locally weighted regression with $\alpha = 0.8$).

3.2. Locations with Significant Trends

We found significant trends at Bakonybél and Felsőtárkány.

At Bakonybél for the full time period we obtained a significant and moderately increasing linear trend ($p = 0.0049$). The LOESS curve fitted fairly well to the linear trend (Table 2, Figure 4).

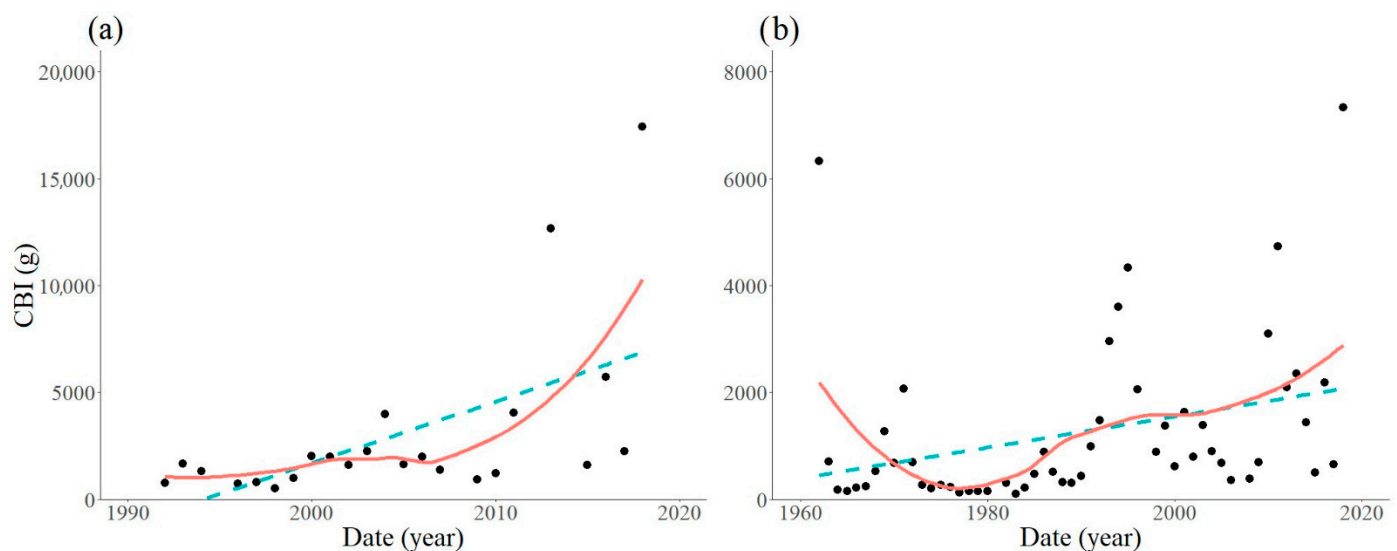


Figure 4. Yearly values and long term trends of the estimated spring caterpillar mass at Bakonybél (a), and Felsőtárkány (b). (CBI, Caterpillar Biomass Index; blue dashed line, linear regression; red line, locally weighted regression with $\alpha = 0.8$).

We found a slightly increasing significant linear trend at Felsőtárkány for the full time range ($p = 0.0202$). The LOESS curve started with a steep decrease in CBI, but from 1977 the curve was constantly increasing (Table 2, Figure 4).

The species responsible for the increase at these two places were four noctuids: *Orthosia cerasi* (F., 1775), *O. gothica*, *O. incerta* (Hufnagel, 1766) and *O. cruda* ((Dennis and Schiffermüller) 1775).

4. Discussion

The values of the calculated spring CBI showed strong year-to-year fluctuations, particularly over the last 2–3 decades, similarly to between-year variability of moth biomass in Britain [36]. This fact makes demonstrating significant trends rather complicated. Our analyses have not revealed any uniform trend at the six trap locations. Four locations showed increasing trends (two significant and two non-significant) and two showed a negative one (both non-significant). None of these datasets supported our preliminary hypothesis about the long term decrease in spring caterpillar abundance. Considering all the locations and time windows together, the overall trend was also increasing rather than decreasing. This contrasts with findings [1,4,37–40] that found declines in diversity and/or biomass of insects. Our results agree more with the conclusions by Macgregor et al. [36] showing that there may have been time periods of either decrease or increase but without a general, strong trend for the whole period analysed.

However, our results do not necessarily mean that some species (even many) are not decreasing, since we analysed the long-term combined abundance trends only of a special group (spring feeding caterpillars). Additionally, although our study locations span Hungary from west to east but to obtain a fully representative picture of the situation in European broad-leaved forests, data from a wider geographical range were needed.

In fact, there are two reasons why further increase in spring caterpillar biomass might be forecasted in Hungarian oak-dominated broadleaved forests. First, it is widely agreed, that as an indirect effect of climate change, the abundance of forest-defoliating insects will increase [10,41–44]. The other reason is the expected change in the status of the Gypsy moth (*L. dispar*). This species is certainly the major defoliator in broadleaved forests of East-Central Europe [45–47]. Its larvae are densely hairy and usually not eaten by birds (and therefore this species was not included in our analysis). However, as a dominant defoliator, it imposes a strong competitive pressure on other spring defoliators on oaks [42] and may limit the abundance of other larvae that are suitable food for invertivorous birds. *Entomophaga maimaiga* Humber, Shimazu and R.S.Soper (Entomophthoraceae), a strongly host specific pathogen of the Gypsy moth [48–50] was released in Bulgaria in 1999 [51], from where it spread to many other Eastern European countries [45,52–54]. This pathogen can cause significant mortality in Gypsy moth populations, as observed in several countries (Bulgaria, Croatia, Hungary, Serbia, Slovakia) in 2013 and 2014. It is forecasted that due to the further spread of this biocontrol agent, Gypsy moth outbreaks in Central Europe will be less intensive and the size of damaged area will decrease [46,55]. The specific insecticide used against the Gypsy moth, *Bacillus thuringiensis* Berliner var. *kurstaki* had beneficial effects on the other folivorous Lepidoptera by reducing the competitive pressure imposed by this moth [56]. In the long term, increasing abundance of other larvae (tortrichids, geometrids, noctuids and even sawflies) may result in more suitable food sources for invertivorous birds.

Numerous long-term datasets are unsuitable to estimate trends, because of varying sampling methods or sampling efforts [57]. The Hungarian Forestry Light Trap Network has a complex history, with many sites not suitable for long-term monitoring due to location changes or trap elimination, but the sampling methods remained identical during the last 60 years. The surroundings of our sampling locations are one another important factor to be mentioned. All six traps were located in mature forested areas (either in forest interior or forest margins). Dramatic environmental changes (large scale deforestation, urbanisation, etc.) did not happen at or around them. These forests can provide diverse and abundant hosts for folivorous lepidopteran species. Large scale chemical insect control is very rare in these Hungarian forests. Consequently, the facts typically held responsible for insect decline in intensively managed agricultural environments do not apply.

Another limitation is that light traps catch only species attracted to light, and of these, only macrolepidopteran species were identified. This means that some important species or species groups could not be included in our analyses. For example, tortricid adults

were not identified, therefore could not be included in this study, although their larvae and pupae are important food for forest dwelling invertivorous birds [58–61].

The peak of the caterpillar biomass in oak dominated forests in Hungary is always in April–May [59]. The predicted increase in spring caterpillar biomass might provide more food for birds in the breeding season but at the same time the increased herbivore pressure may have negative impacts on forest health. This is a major reason why the ecosystem services provided by birds as mass consumers of herbivorous larvae has become an increasingly important issue in forest health [17]. This, however, can be counteracted by the very low availability of suitable nesting holes [62] in these forests. The lack of suitable nesting cavities may limit the forest health-related beneficial ecosystem services that could otherwise be delivered by birds. Quick and widely accepted paradigm shift is necessary to provide sufficient nesting opportunities for forests dwelling invertivorous birds, particularly considering the expected worsening forest health due to increased herbivore pressure by lepidopteran larvae.

5. Conclusions

The analysis of our 23–58 year-long time series, involving 43 lepidopteran species, when converted to an estimate of caterpillar biomass availability in broad leaved forests at six Hungarian locations indicated wide fluctuations but no overall, drastic reduction documented in other European locations. It seems that in south-eastern European, oak-dominated broadleaved forests, the arthropod decline has not occurred; the overall caterpillar biomass has even increased. Due to a rearrangement of the lepidopteran assemblage, some forest health concerns may emerge. In the light of this, it is important to consider how the biocontrol service provided by forest-breeding birds can be maintained or enhanced.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12081070/s1>, Table S1: The list of species included in our analysis, in which months they are present, and their larval size and host plant.

Author Contributions: Conceptualization, G.C.; methodology, G.C., C.B.E. and G.L.L.; formal analysis, C.B.E.; data curation, A.H., C.G. and L.G.; writing—original draft preparation, G.C.; writing—review and editing, C.B.E. and G.L.L.; visualization, C.B.E. and C.G.; project administration, A.H. and G.C.; All authors have read and agreed to the published version of the manuscript.

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