This manuscript is contextually identical with the following published paper:

Bereczki, K., Ódor, P., Csóka, Gy., Mag, Zs., Báldi, A., 2014. Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. Forest Ecology and Management 327: 96–105. DOI: 10.1016/j.foreco.2014.05.001

The original published pdf available in this website:

http://www.sciencedirect.com/science/article/pii/S0378112714002801

Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests

Krisztina Bereczki[a,b*], Péter Ódor[c], György Csóka[d], Zsuzsa Mag[e], András Báldi[b]

Author's affiliation addresses:

[a]Ph.D School of Environmental Sciences, Szent István University, H-2100 Gödöllő, Páter Károly u. 1, Hungary

[b]MTA ÖK Lendület Ecosystem Services Research Group, H-2163 Vácrátót, Alkotmány u. 2-4, Hungary

[c]Institute of Ecology and Botany, MTA Centre for Ecological Research, H-2163 Vácrátót, Alkotmány u. 2-4, Hungary

[d]Department of Forest Protection, Forest Research Institute, H-3232 Mátrafüred, Hegyalja u. 18, Hungary

[e]Department of Plant Systematics, Ecology and Theoretical Biology, Loránd Eötvös University, H-1117 Budapest, Pázmány Péter sétány 1/C, Hungary

*Corresponding author:

Krisztina Bereczki

Present address: MTA ÖK Lendület Ecosystem Services Research Group, H-2163 Vácrátót, Alkotmány u. 2-4, Hungary

Tel.: +36 28 360147/130; fax: +36 28 360110

E-mail address: bereczki.krisztina@okologia.mta.hu (K. Bereczki)

Abstract

Controlling herbivore insects by insectivorous birds is a major ecosystem service, nevertheless little is known about how local habitat features and forest management influence the efficiency of this service and about how the pest control service birds provide can be maintained and improved. We conducted an experiment in temperate oak forests in the Mátra Mountains, northern Hungary to measure bird predation rate of artificial caterpillars resembling winter moth (*Operophtera brumata* L.) larvae, to evaluate the relationships among insectivorous bird communities, caterpillar populations and leaf damage caused by caterpillars and to assess the effect of forest heterogeneity on these processes. We found, that structurally heterogeneous forests maintained a significantly higher abundance of insectivorous birds. Especially the tree size heterogeneity increased bird abundance. The rate of bird predation was positively related to the abundance of insectivorous birds as well as to caterpillar abundance, which indicates that birds were able to respond to caterpillar density. We were not able to demonstrate a direct negative effect of bird predation on caterpillar abundance and a positive effect of caterpillar abundance on leaf damage. Structurally heterogeneous forests, however, suffered from less leaf damage than did homogeneous forests, which result may indicates that the higher activity of insectivorous birds in heterogeneous stands resulted in lower activity of insect herbivores. Thus, we concluded that forest management can contribute to the mitigation of insect damages by maintaining the suitability of forest stands to the insectivorous bird communities through the maintenance of high stand heterogeneity and the presence of some key elements (e.g. retention tree groups, tree diversity, shrub layer).

Key words: ecosystem service; pest control; predation; leaf damage; forest structure; forest management

1. Introduction

Natural ecosystems supply human beings with an array of ecosystem services, without which civilization could not survive (e.g. Sekercioglu, 2010). In addition to their importance in maintaining the health of the ecosystems, most of these services also have a clear economic value (MEA, 2005). One of these economically important services is natural pest control (e.g. Takekawa and Garton, 1984; Kellermann et al., 2008). By consuming pests, natural enemies may act as regulators of pest populations, which may result in the reduction of plant damage (e.g. Sanz, 2001), and thereby reducing economic loss (e.g. Mols and Visser, 2007).

The potential role of natural enemies in the agricultural production has long been recognized. Less attention has been paid to the natural control of forest pests even though forest pests, especially leaf consuming insects, provoke severe damage for forestry worldwide every year (ICP Forest, 2011). In 2005, e.g., herbivorous insects defoliated over 16 million ha of forests in Canada alone (Chang et al., 2009). The situation is similarly serious in Europe, where the proportion of trees with moderate (more than 25 %) defoliation has generally covered more than 20 % of deciduous forests, and has shown a clearly increasing trend (UN-ECE/FAO, 2000). Over the last ten years, the most severely damaged areas have been the Mediterranean and the temperate deciduous oak forests of Central and Eastern Europe (ICP Forest, 2011), where caterpillars are the main defoliators. Their leaf consumption may decrease the growth of trees, negatively influencing their health condition, fecundity, and inhibiting regeneration (Rieske and Dillaway, 2008). The economic value of the wood losses due to reduced growth increases exponentially with the extent of defoliation (Reis et al., 2012), and may reach 310 $/ha/year (Lyytikainen-Saarenmaa and Tomppo, 2002). On top of these significant economic losses, regular insect outbreaks may trigger decline chains in the forests resulting in mass tree mortality (McManus and Csóka, 2007; Jepsen et al., 2013).

Predicted climate change scenarios for Europe foresee more frequent and more severe forest insect outbreaks (Csóka, 1997).

To prevent this large-scale damage, different pest management tactics have been implemented, ranging from non-intervention to area-wide suppression by insecticides (e.g. Zolubas and Ziogas, 2006). In spite of some successful campaigns, it is practically impossible to suppress defoliators over large geographic region by chemical applications (Liebhold, 2012), mainly due to the considerable annual costs (Xue and Tisdell, 2001) and the undesired environmental consequences of pesticide application (Carson, 1962). The recognition of these drawbacks and the increasing public awareness against pesticides has drawn the attention to the role of natural enemies.

The main predators of caterpillars in forests are passerine birds (Kristin and Patocka, 1997), especially during the breeding season, when the proportion of caterpillars in the nestlings' diet can exceed 90% (Seki and Takano, 1998). During the rearing period, a Great Tit (*Parus major* L.) pair preys on approximately 15-20 thousand caterpillars (Török, 1998). Such levels of caterpillar consumption may cause a 20-70% reduction in caterpillar population, indicating a key role of birds in the health of forest ecosystems. However, the abundance of forest birds is highly affected by local factors, especially by forest structure and naturalness (e.g. Fuller, 2003; Hewson, et al., 2011). Consequently, the local habitat features and naturalness of forest ecosystems may influence the trophic interactions between birds and caterpillars. Although the relationship between forest structure and bird abundance (e.g. Freemark and Merriam, 1986; Sekercioglu, 2002; Rosenwald et al., 2011), as well as the predation of caterpillars by birds has been widely examined (e.g. Holmes, 1990; Mols and Visser, 2007), we lack knowledge on how the whole system of forest – birds – caterpillar damage functions and how the service birds provide can be maintained and improved.

In this paper we explored the relationships between the abundance of birds, the abundance of caterpillars, the rate of predation, leaf damage and the effect of forest structure on these processes in temperate deciduous forests. Examining heterogeneous and homogeneous forest stands in pairs, we assumed that heterogeneous forests maintain higher bird abundance than do homogeneous forests, which results in higher predation rate, lower caterpillar abundance and leaf damage. Analysing the examined stands in general (that is heterogeneous and homogeneous stands were pooled for this analysis), we tested the following hypothesis (Fig. 1A): (1) stand structure variables characteristic of natural forests have a positive effect on bird abundance and (2) through the increased bird abundance an indirect negative one on caterpillar abundance; (3) increasing bird abundance increases the predation pressure on caterpillars; (4) higher predation pressure results in lower caterpillar abundance; and finally (5) leaf damage is positively related to caterpillar abundance. The examination of these relationships between the elements of forest ecosystems is needed to adapt the best management to maintain and improve processes which, in turn, provide ecosystem services.

2. Materials and methods

2.1. Study site and experimental design

The experiment was carried out in the southern part of the Mátra Mountains (exact locations are given in Shapiro and Báldi, 2012), in northern Hungary in 2011. The elevation of the study area is between 400-500 m a.s.l.; the topography consists of slopes and narrow valleys. The climate is temperate with a mean annual temperature of 9 °C and an average annual precipitation of 600 mm (Dövényi, 2010). The most common soil type is brown forest soil on an andesite bedrock. This region is covered by deciduous forests dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) and turkey oak (*Q. cerris* L.), which are the two economically most important tree species across the study area with a mixture ratio of 90% (75% of sessile oak and 15% of turkey oak). The insect herbivorous guild of oaks is extremely rich in species in Hungary. As far as is currently known, more than 650 herbivorous insect species feed on oaks, and more than half of them are folivore (unpublished data of Csóka). Among folivore insects, 308 species belong to the Lepidoptera (Csóka and Szabóky, 2005). The monthly abundance of folivore species shows a clear seasonal pattern with a peak of early May or Mid-May, then decline continuously. Their species richness also has a characteristic seasonal pattern; however it peaks later, in late May and early June, and then shows a slow continuous decline. The spring/early summer folivore fauna in the sessile oak stands of mountainous regions is dominated mainly by Geometrid and Noctuid groups, while the late season fauna is dominated by more specialized groups such as leafminers, leafgallers, etc. (Csóka, 1998). Similar differences in folivore community between early and late season was detected in deciduous forests of North-America (Summerville and Crist, 2003). However, in that region the overall folivore abundance and diversity peaks in late July to early August (Marquis and Passoa, 1989).

The selected experimental sites within the study area represented the same habitat type and avoided northern and steep (>25°) slopes and water influenced areas. The age of dominant tree species was above 70 years across the selected sites. Within the study sites, twenty sessile oak tree pairs, i.e. altogether 40 trees were selected in a way that stand age, the average height of the stand and the environmental conditions were similar within the tree pairs, while the forest stand structure was markedly different. One of the pair was in a structurally heterogeneous, the other in a homogeneous stand (Photos of a homogenous and a heterogeneous stand are given in Appendix A). The distinction between heterogeneous and homogenous structural states was a qualitative decision based on the tree species richness, the size distribution of trees, the amount of dead wood, the heterogeneity of tree health conditions, the canopy closure and the shrub (regeneration) layer. The maximum distance between two members of each pair was 500 m, while the distance between two different pairs was 500-2000 m. Spatial autocorrelation was tested using Moran I correlogram and semivariogram and autocorrelation was not observed. The selected tree pairs were situated in forest interior far from the forest edge. Thus, the differences of the studied biological variables between heterogeneous and homogeneous plots were due to the different forest structure.

All of the stands are managed by a state forestry company using shelterwood silvicultural system (rotation period 100-120 years, natural regeneration, regeneration period 5-15 years, cleaning in the young aged stands and thinning in the middle aged stands) but the management had lower intensity in heterogeneous stands. In these stands, the cleaning and thinning were less prevailed than in the homogeneous stands. Furthermore heterogeneous stands were characterized by the presence of over mature trees deriving from the pre-regeneration age group.

2.2. Data collection

Around the selected focal trees, a vegetation assessment was carried out in July and August 2011. The main characteristics measured included tree species composition, tree size distribution, extent of canopy closure, the density of shrubs, understory cover and the availability of dead wood (Table 1). The stand structure and tree species composition was examined in circular plots with a 15 m radius (0.07 ha) around each focal tree. Species identity, diameter at breast height (DBH), basal area, health condition and number of cavities (potential nesting sites) of each tree with DBH larger than 5 cm were recorded. The health condition of a tree was evaluated on an ordinal scale (1-healthy, 2-crown damaged, 3-crown and trunk damaged, 4-dead wood). The stand level health condition was calculated as the mean of the health condition scores of the trees weighted by their relative basal area. Canopy closure was measured with a convex spherical densitometer (Lemmon, 1956). Stand level canopy closure was calculated as the mean of four measurements 7 m away from the focal tree on the four cardinal points. The volume of lying dead wood was measured by line intercept sampling method (Warren and Olsen, 1964), using 3 transect lines of 20 m length at 0, 60, 120 degrees (0 degree to the north). To assess the density of shrub layer (including shrub species and tree seedlings >50 cm height), we divided the shrubs into two size groups. All individuals of shrubs above 1.3 m height were counted in a circle (5.65 m radius) around the focal tree. For the measurement of the shrub density below the height of 1.3 m, the individuals were counted in four 1.5 m radius circular plots located at the four cardinal points 6 m away from the focal tree. The two shrub surveys were combined for the calculation of shrub density (individuals per ha).

To quantify predation rate of caterpillars, we used artificial prey made of green plasticine (Howe et al., 2009) resembling caterpillars of the winter moth (*Operophtera brumata* L.) (Lepidoptera: Geometridae), which is the most common and abundant folivore species of oaks in the study region (Csóka, 1998) and can cause severe defoliation (Tikkanen et al., 1998). The applied method does not provide an estimation of the natural predation rate but it may allow us to measure differences among habitats (González-Gómez et al., 2006; Howe et al., 2009). Fifteen artificial caterpillars were attached to the branches of each focal tree (in total 600 caterpillars) on 13 May 2011 during the peak abundance of Geometrid species. The size of artificial caterpillars was approximately equal to the size of a fifth instar winter moth larva (length 25 mm, diameter 3.5 mm; Fig. 2A). The artificial caterpillars were glued towards the end of branches near the leaves at 1.5 m - 2.5 m height. The minimum distance between caterpillars was approximately 0.5 m. We checked the plasticine caterpillars on every second day (15, 17 and 19 May 2011); caterpillars showing marks of predation were removed. After six days (19 May), all caterpillars were removed. This six day duration proved to be the optimal prey exposure length calibrated by preliminary experiments. The level of predation was expressed as the percentage of damaged caterpillars during this six days period. During the analysis, only marks caused by birds were taken into account (a photo of a beak mark is shown in Fig. 2B).

To estimate the abundance of bird species, we used a 10 minute point count method (Gregory et al., 2004) around each focal tree within a 100 m radius. The counting was conducted between 05.00 and 09.00 h once during the caterpillar exposure period. All observed or heard individuals were recorded. During the analysis we excluded bird species that do not prey upon caterpillars (Cramp, 1998; see Appendix B for the list of recorded bird species). The abundance was expressed as the total number of recorded individuals per plot.

The abundance of real caterpillars was measured by collecting foliage samples from sessile oak trees during the experimental period. Five trees within a 20 m radius of the focal trees were randomly selected. On each selected tree, one branch of approximately 30 cm of length was cut with a pole branch cutter at a height of 3-4 m. Before cutting, we placed a canopy net over the selected branch to avoid the escape of caterpillars. The collected samples were put into plastic bags and were brought to the laboratory where caterpillars were identified to the species level (see Appendix C). The abundance of caterpillars was assessed as the number of individuals per 100 leaves.

Leaf damage was estimated on the same leaf samples (see details above). All leaves per sample were evaluated as damaged or not. A leaf was considered as damaged if it showed any sign of herbivory. The leaf damage per plot was assessed as the proportion of damaged leaves.

2.3. Data analysis

To give a quantitative substantiation of our qualitative assignment of heterogeneous and homogeneous forest sites, a linear discriminant analysis (LDA) was conducted (Borcard et al., 2009). To investigate the differences of biological variables (stand structural variables, bird abundance, caterpillar abundance, predation rate, and leaf damage) between the two members of the pairs (heterogeneous and homogenous), we used a paired Student's t-test. The data were tested whether the assumptions of the parametric statistic (normal distribution, homogeneity of variance) were fulfilled.

General linear mixed regression models (GLMM) were built for estimating the relationship between bird and caterpillar abundance and forest structural variables (Zuur et al., 2009). We used a standardized value (zero mean, one standard deviation) of forest structural variables as fixed and plot pairs as a random factor. Before modelling, we carried out pairwise correlation analyses and graphical explorations between the dependent variables and the potential explanatory variables. We also checked inter-correlations among explanatory variables. Only explanatory variables that significantly correlated with the dependent variables, had homogenous scatterplots, and had low inter-correlations with other explanatory variables ($r_{abs} < 0.35$) were retained in the linear model selection. Fixed effect selection of the full model was made by backward elimination, during which the maximum likelihood method was used. The random effect was tested by restricted maximum likelihood method (Faraway, 2006). During model evaluation, we took into account the graphical diagnostics of the models (relative weight of samples, normality of residuals, and homogeneity of variety of residuals) in addition to the results of statistical testing.

The relationship between predation rate and bird abundance, between caterpillar abundance and predation rate and finally between leaf damage and caterpillar abundance was also examined by GLMM. All of the three models plot pairs were used as random factor. We also calculated the correlation coefficients between the studied variables.

All tests were carried out in R 2.13.0 environment (R Development Core Team, 2011). We used the package “nlme” (Pinheiro et al., 2011) for the GLMM analysis and package “MASS” (Venables and Ripley, 2002) for the LDA analysis.

3. Results

3.1. Predation rate, bird and caterpillar abundance and leaf damage

The recorded mean (± SD) predation rate of artificial caterpillars was 27.5% (SD = 13.77, n = 40), of which 80.9% (SD = 11.69, n = 40) was bird predation. Mandible marks of chewing arthropods were found on 43.2% (SD = 12.26, n = 40) of the artificial preys, while 1.2% (SD = 0.41, n = 40) of marks remained unidentified. 25.3% (SD = 7.24, n = 40) of caterpillars showed more than one marks.

We detected a total of 31 bird species from all study sites, of which 26 species were insectivores, i.e. potential predator of caterpillars. We included only the 26 insectivorous species in the analysis (see Appendix B). The mean abundance of insectivorous birds was 7.58 (SD = 3.86, n = 40) individuals per plot and the mean species richness was 5.28 (SD = 1.94, n = 40) insectivorous bird species per plot. The most abundant insectivorous bird species were the Common Chaffinch (*Fringilla coelebs* L.), the Eurasian Blackcap (*Sylvia atricapilla* L.), the Great Tit (*Parus major* L.) and the Blue Tit (*Cyanistes caeruleus* L.).

We identified larvae of 19 lepidopteran and 1 hymenopteran species (see Appendix C). The mean standardized abundance of caterpillars was 1.28 (SD = 0.52, n = 40) per 100 leaves and the mean species richness was 0.71 (SD = 0.26, n = 40) species per 100 leaves. The caterpillars with the highest abundance belonged to the families Tortricidae and Geometridae. Within the family Tortricidae, *Archips xylosteana* L. and *Choristoneura heibenstreitella* Müller were the most abundant. Within the family Geometridae, *Agriopis aurantiaria* L. and the winter moth were dominant species.

The mean proportion of damaged leaves was 0.49 (SD = 0.14, n = 40).

3.2. Differences between heterogeneous and homogeneous sites

The separation of heterogeneous and homogeneous stands based on LDA was appropriate. The apriori and aposteori classification was the same in the 85% of the objects. The detailed results of the LDA as well as the detailed examination of the misclassifications (6 sites from the 40) are shown in Appendix D.

Table 1 shows the significant structural differences between the heterogeneous and homogeneous forest sites based on Student's t -test. In heterogeneous stands, the density of large trees, tree size heterogeneity, shrub density, shrub diversity and the density of cavities were higher than in homogenous stands (p = <0.001 – 0.029). Mean tree size, tree density, the volume of dead wood, the degree of canopy closure and tree health conditions were similar between heterogeneous and homogeneous stands (p = 0.127 – 0.837, all NS).

Heterogeneous forests also supported a significantly higher abundance of insectivorous birds than homogenous forests did (Table 2). The predation rate and the abundance of caterpillars did not significantly differ between the two study site types. However, leaf damage was higher in homogenous than in heterogeneous stands (Table 2).

3.3. Explanatory variables

Forest structure considerably affected the abundance of insectivorous birds: tree size heterogeneity (variation coefficient of DBH) noticeably increased bird abundance (GLMM, estimate: 2.37, Log.Ratio = 18.13, $p < 0.0001$), while tree species richness had a marginally positive effect (GLMM, estimate: 0.87, Log.Ratio = 2.90, $p = 0.089$). Caterpillar abundance was not influenced by structural variables of stands (no significant fixed effect in GLMM).

GLMM revealed a positive linear correlation between predation rate and bird abundance (r = 0.366, Fig. 3A). Bird abundance significantly increased the predation pressure (estimate = 0.167, Log.Ratio = 5.70, $p = 0.017$). Contrary to our hypothesis, that predation has a negative effect on caterpillar abundance, we found a positive correlation between predation and caterpillar abundance (r = 0.378, Fig. 3B), as well as a significant positive effect of caterpillar abundance on predation (estimate = 1.282, Log.Ratio = 6.33, $p = 0.021$). Caterpillar abundance did not significantly influence leaf damage (GLMM, estimate = 0.067, Log.Ratio = 2.49, $p = 0.115$).

Comparing our hypothesis with the results (Fig. 1), the positive effect of forest heterogeneity on bird abundance and bird abundance on predation were supported. However, the negative effect of forest heterogeneity on caterpillar abundance and the positive effect of caterpillar abundance on leaf damage were rejected; we did not find significant relationships between these variables. We expected a negative effect of predation on caterpillar abundance but we found an opposite relationships, caterpillar abundance increased predation.

4. Discussion

In our study, insectivorous birds were responsible for the largest proportion of predation on artificial caterpillars. Thus, the maintenance of the high density of bird assemblages is of key importance (Sekercioglu, 2010). The abundance of insectivorous birds was higher in heterogeneous than in homogenous forest stands. The most important explanatory factors of insectivorous bird abundance proved to be tree size heterogeneity. That is birds benefited from the presence of different age and size groups of trees. According to the former studies (e.g. Fuller, 2003; Diaz, 2008), especially the presence of large, older trees (>40 cm) have a positive effect on bird abundance, because older trees generally have more diverse strata composition than younger trees, and thereby provide more feeding grounds, refuges and breeding sites. In particular, birds that nest in natural cavities are rewarded by large trees, as they generally select nest trees thicker than 25 cm DBH (Lawler and Edwards, 2002). Because cavity nesting birds are the most important predators of caterpillars, the presence of large trees has a key role to maintaining service birds provide. In heterogeneous stands (in that bird abundance was higher) density of large trees, tree size heterogeneity and number of cavities were significantly higher than on homogenous ones. In addition to tree size heterogeneity, tree species richness also had a positive effect on bird abundance, although this effect was only marginal. The positive effect of tree species richness may be explained by increased herbivore diversity, which may result in greater stability of food supply for insectivorous birds (Laiolo, 2002). On the other hand, tree species diversity generates structural diversity which may have a positive effect on bird abundance as well as on bird species richness (Hinsley et al., 2009).

In accordance with our hypothesis, an increase in bird abundance resulted in higher predation rate. This result overlaps with earlier studies that found linear relationship between predator abundance and predation rate (e.g. González-Gómez et al., 2006). Thus, we conclude that predation pressure on caterpillars primarily depends on the abundance of insectivorous birds. But how does this increasing predation pressure affect caterpillar abundance? We hypothesized that high predation level lead to decreasing caterpillar abundance, which was supported by the results of numerous cage experiments (e.g. Tanhuanpää et al., 2001; Schwenk et al., 2010). Contrary to our hypothesis, we were not able to directly demonstrate the negative effect of bird predation on caterpillar abundance. Thus, caterpillar abundance was directly influenced neither by the forest structure, nor by the predation pressure. The lack of the negative effect of predation pressure on caterpillar population may be explained by the synoptic population model of Southwood and Comins (1976). According to this model, the restriction effect of generalist predators – like insectivorous birds – cannot be manifested at high prey densities, at which other mortality factors, such as starvation and diseases cause the population to collapse (Southwood and Comins, 1976). Thus, the role of insectivorous birds is not to depress high caterpillar populations, but to maintain caterpillar abundance at low or moderate densities and thereby to extend the period between outbreaks (e.g. Holmes, 1990; Sekercioglu, 2010).

Contrary to our hypothesis we found an inverse relationship between predation rate and caterpillar abundance. That is predation rate was positively related to caterpillar abundance. As the predation rate primarily depends on bird abundance, this is a result consistent with former ideas, according which birds exhibit numerical response to prey density (e.g. Holmes, 1990; Mantyla et al., 2008). In other words, the bird abundance and thereby the predation pressure is higher in areas, where the caterpillar density is high. Although this high predation pressure did not lead to the decreasing of caterpillar population, the presence of an abundant bird community may hinder the further growth of caterpillar abundance. However, it should be mentioned that our study was a short-term experiment, thus we cannot conclude on the long-term changes of caterpillar abundance.

Although we failed to directly demonstrate the negative effect of bird predation on caterpillar population, we found that heterogeneous forests, which maintained higher bird abundance, had lower leaf damage than homogeneous forests. This indirect effect of forest structure and different management types on the damage caused by herbivores was also demonstrated by former studies (e.g. Moore et al., 1991). In our case, however, the caterpillar abundance did not differed between the two stand types and we did not found any significant relationship between caterpillar abundance and leaf damage. We set up five alternative explanations for this lack of relationship. First, leaf damage caused by herbivores can be depended not only on the abundance of herbivores, but also on the feeding activity of them. The feeding activity of herbivores can be influenced by the presence of predator species (McArthur et al., 2012) or by the quality of plant material which they feed on (e.g. Coley et al., 2006). The quality of plant material, in turn, can be altered by different growing conditions as well as by different management types (Forkner and Marquis, 2004). Thus, it is possible, that our plots differed in leaf quality. Second, the high density of shrubs in heterogeneous stands may decrease the herbivore pressure on oaks by providing other source for herbivores. Third, larger caterpillars, such as some Noctuid species spend most of their times on tree trunks or on thick branches during daytime (Stamp and Casey, 1993), thus they are less likely to be sampled by cutting the end of branches. Fourth, larger caterpillars may have pupated before our sampling; however the sign of their herbivory was remained. Finally, our way of characterising herbivore damage by the number of damaged leafs, could be a less accurate estimate of leaf damage than measuring the missing leaf surface. Thus, the lack of the expected relationship between caterpillars and leaf damage may also be traced back to methodological reason. To examine the above-mentioned alternative hypothesis in detail, further research is needed.

5. Conclusions

Our study pointed out how important relationships are formed among the elements of the forest ecosystems (forest stand characteristics, bird and caterpillar assemblages), which are linked by the processes of predation and herbivory. In the recent study, forest structural heterogeneity directly influenced the abundance of insectivorous birds, and thereby had an indirect effect on bird predation. The high bird predation pressure did not result in lower caterpillar abundance. Structurally heterogeneous forests, however, suffered from less leaf damage than did homogeneous forests, which result may indicates that the higher activity of insectivorous birds in heterogeneous stands resulted in lower activity of insect herbivores. Summarizing, the forest heterogeneity did not affect the abundance of caterpillar pest populations, but it had an indirect effect on leaf damage caused by herbivore insects. Thus, we conclude that forest management can significantly contribute to the mitigation of insect damages by maintaining the suitability of forest stands to the insectivorous bird communities through the maintenance of high stand heterogeneity.

European oak dominated forests are mainly managed by shelterwood silvicultural system, which results in basically even-aged homogeneous stands with low density of shrub layers (Matthews, 1991). Within this silvicultural system, the stand level heterogeneity can be increased by the spatially heterogeneous, finer scale implementation, by the maintenance of retention tree groups and by the extension of regeneration period. In Hungary, moreover, a significant progress has been made to the continuous forest cover forestry during the last years (Frank, 2000). This management practice includes the tree selection system, which results in an uneven-aged type of stand in which all the age and size classes are mixed together. In the present study, tree size heterogeneity proved to be the most important explanatory variables of insectivorous bird abundance, thus the management practice ensuring this type of heterogeneity can contribute significantly to the self-protecting ability of forest stands against insect damages. Nevertheless, the tree selection system is more advanced in the zone of beech forests. The wide range application of this management practice in oak forests would ensure more heterogeneous stands, which would be beneficial in terms of natural pest control.

Acknowledgements

We thank the foresters and private landowners for allowing use of the study sites, Gábor L. Lövei for providing methodological advice on the technique and for commenting on the manuscript, Anikó Kovács, Csaba Simon and Anna Pálfy for their help in field work, Julie Teresa Shapiro for comments to improve this manuscript and correct the English. The study was financially supported by the "Lendület" project of the Hungarian Academy of Science, by the OTKA NN 101940 project, and by TÁMOP-4.25.2.A-11/1/KONV (to GC). Péter Ódor was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences.

Appendices

Appendix A.

Photos of a homogeneous and a heterogeneous stand.

Appendix B.

The list of the recorded bird species and the mean (SD) number of individuals per species in heterogeneous and homogeneous sites in the Mátra Mountains, Hungary.

Appendix C.

The list of the recorded caterpillars and the mean (SD) number of individuals per 100 leaves in heterogeneous and homogeneous sites in the Mátra Mountains, Hungary.

Appendix D.

Detailed results of the linear discriminant analysis (LDA).

References

Borcard, D., Gillet, F., Legendre, P., 2009. Numerical Ecology with R. New York: Springer.

Carson, R., 1962. Silent Spring. Boston: Houghton Mifflin.

Chang, W.Y., Lantz, V.A., MacLean, D.A., 2009. Public attitudes about forest pest outbreaks and control: Case studies in two Canadian provinces. Forest Ecology and Management 257, 1333–1343.

Coley, P.D., Bateman, M.L., Kursar, T.A., 2006. The effects of plant quality on caterpillar growth and defense against natural enemies. Oikos 115, 219–228.

Cramp, S., 1998. The Complete Birds of the Western Palearctic on CD-ROM. Oxford: Oxford CD-ROM.

Csóka, Gy., 1997. Increased insect damage in Hungarian forests under drought impact. Biologia 52, 1–4.

Csóka, Gy., 1998. Oak defoliating insects in Hungary. In: McManus, M.L., Liebhold, A.M. (Eds.), Proceedings: Population Dynamics, Impacts and Integrated Management of Forest Defoliating Insects. USDA Forest Service General Technical Report NE-247, pp. 334–335.

Csóka, Gy., Szabóky, Cs., 2005. Checklist of Herbivorous Insects of Native and Exotic Oaks in Hungary I. Acta Silvatica et Lignaria Hungarica 1, 59–72.

Diaz, L., 2008. Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain. Forest Ecology and Management 223, 54–65.

Dövényi, Z., 2010. Magyarország Kistájainak katasztere. (Cadastre of Hungarian regions). Budapest: MTA Földrajztudományi Kutatóintézet. Hungary.

Faraway, J.J., 2006. Extending the Linear Model with R. London: Chapman and Hall.

Forkner, R.E., Marquis, R.J., 2004. Uneven-aged and even-aged logging alter foliar phenolics of oak trees remaining in forested habitat matrix. Forest Ecology and Management 199, 21–37.

Frank, T. 2000. Természet – Erdő – Gazdálkodás (Nature – Forest – Management). BirdLife Hungary. Eger: Pro Silva Hungaria Society. Hungary.

Freemark, K.E., Merriam, H.G., 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36, 115–141.

Fuller, R.J., 2003. Bird Life of Woodland and Forest. Cambridge: Cambridge University Press.

González-Gómez, P.L., Estades, C.F., Simonetti, J.A., 2006. Strengthened insectivory in a temperate fragmented forest. Oecologia 148, 137–143.

Gregory, R.D., Gibbons, D.W., Donald, P.F., 2004. Bird census and survey techniques. In: Sutherland, W.J., Newton, I., Green, R.E. (Eds.), Bird Ecology and Conservation – A handbook of techniques. Oxford: Oxford University Press, pp. 17–56.

Hinsley, S.A., Hill, R.A., Fuller, R.J., Bellamy, P.E., Rothery, P., 2009. Bird species distributions across woodland canopy structure gradients. Community Ecology 10, 99–110.

Hewson, C.M., Austin, G.E., Gough, S.J., Fuller, R.J., 2011. Species-specific responses of woodland birds to stand level habitat characteristics: The dual importance to forest structure and floristics. Forest Ecology and Management 261, 1224–1240.

Holmes, R.T., 1990. Ecological and evolutionary impacts of bird predation on forest insects: an overview. In: Morrison, M.L., Ralph, J.J., Verner, J., Jehl, J.R. (Eds.), Avian Foraging: Theory, Methodology, and Applications. Lawrence: Allen Press, pp. 6–13.

Howe, A., Lövei, G.L., Nachman, G., 2009. Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomologia Experimentalis et Applicata 131, 325–329.

ICP Forest (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests). 2011. The Condition of Forests in Europe. Executive Report. Hamburg: Institute for World Forestry. <http://www.icp-forests.org> (accessed October 2012).

Jepsen, J.U., Biuw, M., Ims, R.A., Kapari, L., Schott, T., Vindstad, O.P.L., Hagen, S.B., 2013. Ecosystem Impacts of a Range Expanding Forest Defoliator at the Forest-Tundra Ecotone. Ecosystems 16, 561–575.

Kellermann, J.L., Johnson, M.D., Stercho, A.M., Hackett, S.C., 2008. Ecological and Economic Services Provided by birds on Jamaican Blue Mountain Coffee Farms. Conservation Biology 22, 1177–1185.

Kristin, A., Patocka, J., 1997. Birds as predators of Lepidoptera: Selected examples. Biologia 52, 319–326.

Laiolo, P., 2002. Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy. Folia Zoologica 51, 121–128.

Lawler, J.J., Edwards, T.C., Jr. 2002. Composition on cavity-nesting bird communities in montane aspen woodland fragments: The roles of landscape context and forest structure. The Condor 104, 890–896.

Lemmon, P.E., 1956. A spherical densiometer for estimating forest overstorey density. Forest Science 2, 314–320.

Liebhold, A.M., 2012. Forest pest management in changing world. International Journal of Pest Management 58, 289–295.

Lyytikainen-Saarenmaa, P., Tomppo, E., 2002. Impact of sawfly defoliation on growth of Scots pine Pinus sylvestris (Pinaceae) and associated economic losses. Bulletin of Entomological Research 92, 137–140.

Mantyla, E., Alessio, G.A., Blande, J.D., Heijari, J., Holopainen, J.K., Laaksonen, T., Piirtola, P., Klemola, T., 2008. From Plants to Birds: Higher Avian Predation Rates in Trees Responding to Insect Herbivory. PlosOne 3, e2832.

Marquis R.J., Passoa, S. 1989. Seasonal diversity and abundance of the herbivore fauna of striped maple Acer pensylvanicum L. (Aceraceae) in western Virginia. American Midland Naturalist 122, 313–320.

Matthews, J.D., 1991. Silvicultural Systems. Oxford: Oxford University Press.

McArthur, C., Orlando, P., Blanks, P.B., Brown, J.S., 2012. The foraging tightrope between predation risk and plant toxins: a matter of concentration. Functional Ecology 26, 74–83.

McManus, M., Csóka, Gy., 2007. History and Impact of Gypsy Moth in North America and Comparison to the Recent Outbreaks in Europe. Acta Silvatica et Lignaria Hungarica 3, 47–64.

MEA (Millennium Ecosystem Assessment). 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. Washington: World Resources Institute.

Mols, C.M.M., Visser, M.E., 2007. Great Tits (Parus major) Reduce Caterpillar Damage in Commercial Apple Orchards. PlosOne 2, e202.

Moore R., Warrington, S., Whittaker, J.B., 1991. Herbivory by insects on oak trees in pure stands compared with paired mixtures. Journal of Applied Ecology 28, 290–304.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., The R Development Core Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models. R package version. 3, 1–102.

R Development Core Team. 2011. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org/>.

Reis, A.R., Ferreira, L., Tomé, M., Araujo, C., Branco, M., 2012. Efficiency of biological control of *Gonipterus platensis* (Coleoptera: Curculionidae) by *Anaphes nitens* (Hymenoptera: Mymaridae) in cold areas of the Iberian Peninsula: Implications for defoliation and wood production in *Eucalyptus globulus*. Forest Ecology and Management 270, 216–222.

Rieske, L.K., Dillaway, D.N., 2008. Response of two oak species to extensive defoliation: Tree growth and vigor, phytochemistry, and herbivore suitability. Forest Ecology and Management 256, 121–128.

Rosenwald, R., Lohmus, A., Kraut, A., Remm, L., 2011. Bird communities in hemiboreal old-growth forest: The roles of food supply, stand structure and site type. Forest Ecology and Management 262, 1541–1550.

Sanz, J.J., 2001. Experimentally increased insectivorous bird density results in a reduction of caterpillar density and leaf damage to Pyrenean oak. Ecological Research 16, 387–394.

Schwenk, W.S., Strong, A.M., Sillet, T.S., 2010. Effects of bird predation on arthropod abundance and tree growth across an elevational gradient. Journal of Avian Biology 41, 367–377.

Sekercioglu, C.H., 2002. Effects of forestry practice on vegetation structure and bird community of Kibale National Park, Uganda. Biological Conservation 107, 229–240.

Sekercioglu, C.H., 2010. Ecosystem functions and services. In: Sodhi, N.S., Ehrlich, P.R. (Eds.), Conservation Biology for All. Oxford: Oxford University Press, pp. 45–72.

Seki, S.I., Takano, H., 1998. Caterpillar abundance in the territory affects the breeding performance of great tit Parus *major minor*. Oecologia 114, 514–521.

Shapiro, J.T., Báldi, A., 2012. Lost locations and the (ir)repeatability of ecological studies. Frontiers in Ecology and the Environment 10, 235–236.

Southwood, T.R.E., Comins, H.N., 1976. A synoptic population model. Journal of Animal Ecology 45, 949–965.

Summerville, K.S., Crist, T.O., 2003. Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: Roles of season, eco-region and patch size. Oikos 100,134–148.

Stamp, N.E., Casey, T.M., 1993. Caterpillars – Ecological and Evolutionary Constraints on Foraging. London: Chapman & Hall, pp. 231–232.

Takekawa, J.Y., Garton, E.O., 1984. How much is an evening grosbeak worth? Journal of Forestry 82, 426–428.

Tanhuanpää, M., Ruohomaki, K., Uusipaikka, E., 2001. High larval predation rate in non-outbreaking populations of a geometrid-moth. Ecology 82, 281–289.

Tikkanen, O.P., Roininen, H., Niemelä, P., Tahvanainen, J., Zinovjev, A., 1998. Use of host plants by Operophtera brumata L. (Lep., Geometridae) during the first recorded outbreak in the subcontinental boreal zone of Fennoscandia. Journal of Applied Entomology 122, 247–253.

Török, J., 1998. Great Tit. In: Haraszthy, L. (Ed.), Magyarország Madarai (Birds of Hungary). Budapest: Mezőgazda Kiadó, Hungary, p. 336.

UN-ECE/FAO (United Nations Economic Commission for Europe Food and Agriculture Organization of the United Nations). 2000. Forest Resources of Europe, CIS, North-America, Australia, Japan and New Zealand. United Nations: Geneva Timber and Forest Study Papers, N-17.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. New York: Springer.

Warren, W.G., Olsen, P.F., 1964. A line intersect technique for assessing logging waste. Forest Science 10, 267–276.

Xue, D., Tisdell, C., 2001. Valuing ecological functions of biodiversity in Changbaishan Mountain Biosphere Reserve in Northeast China. Biodiversity and Conservation 10, 467–481.

Zolubas, P., Ziogas, A., 2006. Insect damage in Lithuania: Experience from the recent outbreaks. In: Csóka, Gy., Hirka, A., Koltay, A. (Eds.), Biotic damage in forests. Proceedings of the IUFRO Symposium. Hungarian Forest Research Institute. Budapest: Agroinform Publishing House, Hungary, pp. 340–344.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G., 2009. Mixed Effects Models and Extension in Ecology with R. New York: Springer.

Tables:

Table 1

The mean (SD) of the structural variables in heterogeneous and homogenous forest sites and the significance of the differences between the two site types in the Mátra Mountains, Hungary[a].

Forest characteristic	Mean (SD) in heterogeneous sites	Mean (SD) in homogenous sites	t_{19}	*p*
Tree species composition				
Tree species richness (number of species/plot)	3.15 (1.14)	2.90 (1.17)	0.72	0.240
Stand structure				
Density of all trees (stems/ha)	718.57 (421.29)	780.00 (304.93)	0.62	0.729
Density of large trees (DBH>40 cm) (stems/ha)	30.71 (37.73)	7.86 (14.27)	2.63	0.008
Basal area (m^2/ha)	29.40 (6.94)	30.61 (8.82)	0.61	0.726
Mean DBH (cm)	22.68 (5.99)	22.14 (5.44)	0.47	0.320
Tree size heterogeneity (Coefficient of variation of DBH)	108.42 (96.17)	41.54 (26.73)	2.99	0.004
Amount of dead wood (m^3/ha)	12.58 (13.67)	8.46 (7.56)	1.18	0.127
Number of cavities per plot	1.10 (2.25)	0.10 (0.31)	2.01	0.029
Canopy closure (%)	87.79 (7.84)	89.78 (7.67)	1.00	0.837
Health condition (health condition scores of the trees weighted by their relative basal area)	1.52 (0.30)	1.55 (0.31)	0.46	0.676
Shrubs and understorey				
Density of shrubs (stems/ha)	10298.47 (5056.08)	3790.82 (4023.90)	4.87	<0.001
Number of shrubs (species/plot)	8.75 (3.46)	4.90 (4.36)	3.73	<0.001
Cover of shrubs (%)	38.25 (16.16)	19.30 (23.02)	3.10	0.003
Cover of understorey layers (%)	59.00 (18.04)	55.75 (20.47)	0.51	0.308

[a] We used paired Student's t-test to test the significance.

Table 2

The mean (SD) of the examined biological variables in heterogeneous and homogeneous forest sites and the significance of the differences between the two site types in the Mátra Mountains, Hungary[a].

Biological variables	Mean (SD) in heterogeneous sites	Mean (SD) in homogeneous sites	t_{19}	p
Bird abundance[b]	8.75 (4.39)	6.40 (2.87)	2.02	0.029
Predation rate[c]	21.33 (11.36)	22.33 (12.29)	0.28	0.607
Caterpillar abundance[d]	1.31 (0.60)	1.26 (0.44)	0.46	0.324
Leaf damage[f]	0.45 (0.14)	0.53 (0.13)	2.03	0.024

[a] We used paired Student's t-test to test the significance.

[b] The number of insectivorous birds within the 100 m radii study plots.

[c] The % of the artificial caterpillars attacked by insectivorous birds on the focal trees.

[d] The number of lepidoptera larvae per 100 leaves within the 15 m radii study plots.

[e] The proportion of the damaged leaves within the 15 m radii study plots.

Figures

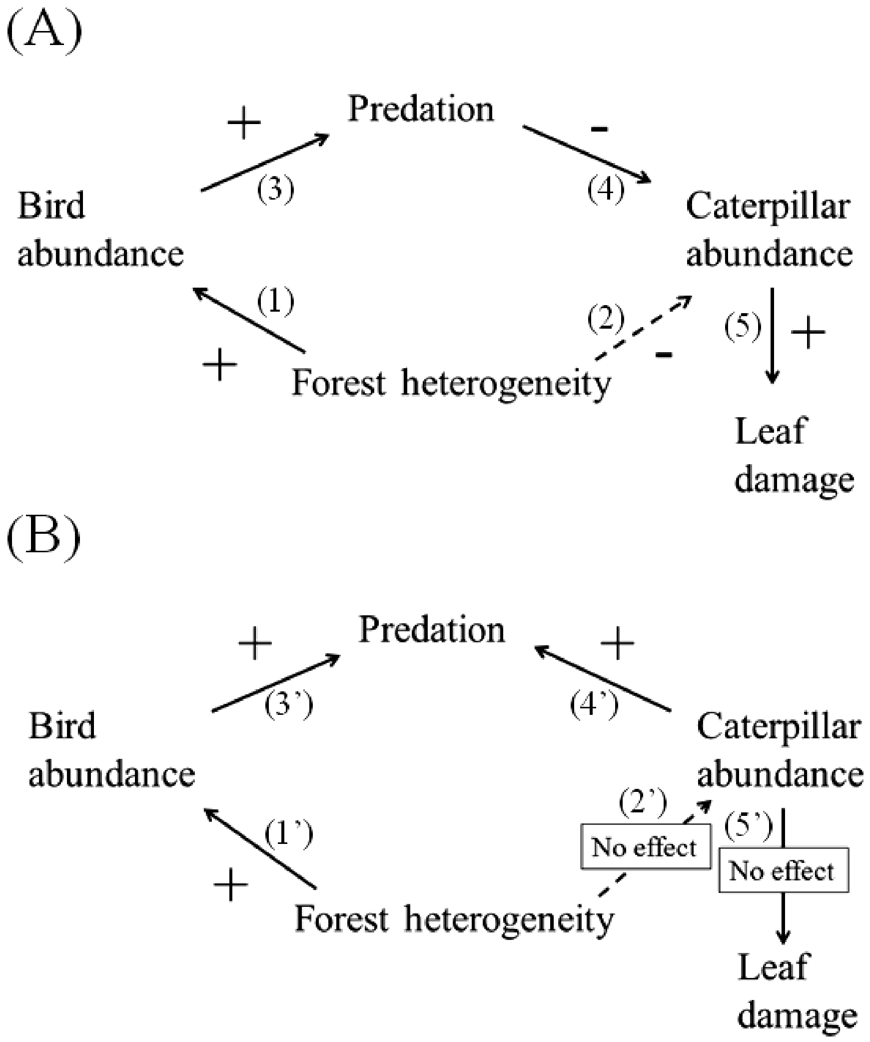

Fig. 1. The hypothesized effects of the studied system in temperate oak forests (A), and the effects between the elements according to our results (B). The arrows show the direction of the hypothesized and the detected effects between the elements of the studied system. The different arrow types represent direct (solid line) or indirect (dashed line) interactions. + indicates positive effect, - indicate negative effect, while no effect means no significant effect was found. The tested hypotheses were the following: forest heterogeneity increases bird abundance (1) and decreases caterpillar abundance (2), predation rate is positively related to bird abundance (3), increased predation rate decreases caterpillar abundance (4) and

caterpillar abundance positively affects the leaf damage (5). The effects between the elements according to our results in temperate oak forest in Hungary: forest heterogeneity increased bird abundance (1') but had no effect on caterpillar abundance (2'), predation rate was positively related to bird abundance (3') and to caterpillar abundance (4'), leaf damage was not affected by caterpillar abundance (5').

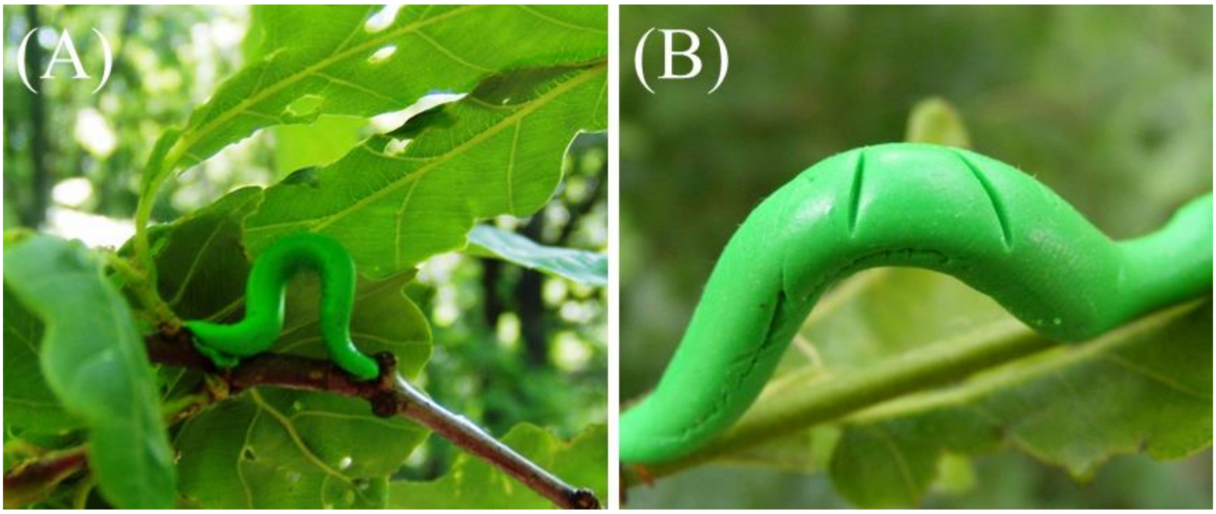

Fig. 2. An artificial caterpillar attached to the branches of sessile oak (*Quercus petraea*) (A), and a beak mark on artificial caterpillar (B).

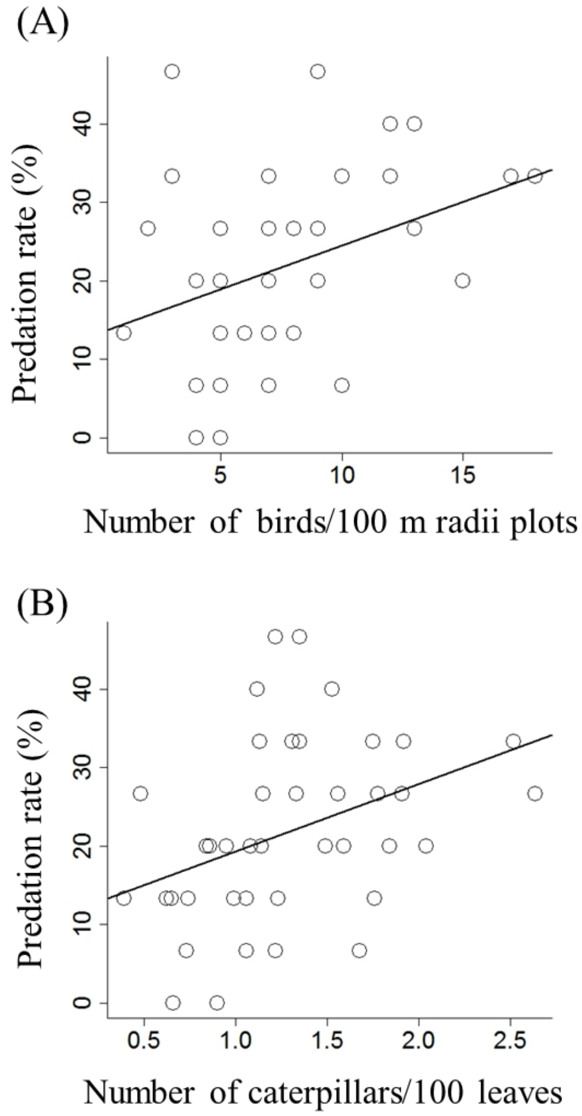

Fig. 3. Correlations between predation rate and bird abundance (r = 0.366, $p < 0.02$) (A), and between predation rate and caterpillar abundance (r = 0.378, $p < 0.02$) (B) in temperate oak forests in the Mátra Mountains, Hungary.