Can Late Flushing Trees Avoid Attack by Moth Larvae in Temperate Forests?

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Abstract


We investigated moth larvae (Lepidoptera) developing in temperate forests in Central Europe shortly after the tree budburst (the “brumata-viridana complex”). Larvae were collected in southern Slovakia in May 2015 and May 2016 from young and mature trees of late flushing Quercus cerris L. and early flushing Q. pubescens Willd. Although Q. cerris yielded fewer species (40 species) than Q. pubescens (47 species), the rarefied number of species and the Chao index suggested a similar number of species on mature trees of both oak species. Both the total number of moth larvae in assemblages and the abundance of dominant species (pests) were significantly lower on Q. cerris than Q. pubescens.

The results suggest the release of Q. cerris with delayed budburst from heavy infestations by folivorous moth larvae. Knowledge obtained can be applied in silvicultural and horticultural practices aimed to protect and maintain forest, fruit, and ornamental trees.

Keywords: Quercus cerris; Quercus pubescens; folivorous insects; Lepidoptera; phenology; budburst

Phenological synchrony between the hatching of folivorous larvae and the budburst of their host plants is crucially important for the fitness of many spring insect herbivores (Tikkanen & Julkunen-Tittoo 2003). This phenomenon has been documented in many lepidopteran species (Du Merle 1988; Hunter 1990, 1992; Van Dongen et al. 1997; Hunter & Elkinton 2000; Tikkanen & Lyytikäinen-Saarenmaa 2002). Recently, greater attention has been paid to the asynchrony (or mismatch) between insects and their host plants to reveal impacts of global warming on interspecific interactions (Visser & Holleman 2001; Van Asch et al. 2007; De Vries et al. 2011; Foster et al. 2013; Wagenhoff et al. 2013; Martemyanov et al. 2015; Despland 2018). The phenological asynchrony between insect herbivores and their hosts may modify the patterns of defoliation in temperate forests (Foster et al. 2013).

There are two types of asynchrony between the hatching of folivorous moth larvae and the tree budburst: (1) larvae hatch later – when leaves are relatively old and already well developed; (2) larvae hatch early – when leaves are not present as buds are still closed. In both cases, the larvae can disperse to suitable feeding sites using ballooning, lowering or walking (Holliday 1977; Hunter 1990; Zalucki et al. 2002). Despland (2018) but their success in finding a suitable host is not clear (Zalucki et al. 2002). Negative effects of old leaves or low quality food on the late occurring larvae are well known (e.g. Feeny 1968, 1970; Raupp et al. 1988; Hunter & Lechowicz 1992; Tikkanen & Julkunen-Tittoo

2003; Jones & Despland 2006; Martemyanov et al. 2015). Several authors reported more extensive defoliation by insect herbivores on early rather than late flushing trees (Hunter 1992; Ovcharov et al. 2000; Wesołowski & Rówiński 2008; Mannai et al. 2017). Folivorous insect assemblages have not yet been described and compared between early and late flushing trees in complexity, and effects of late budburst on species assemblages remain unknown. Oak species (Quercus spp.) differing in the timing of budburst are ideally suited to fill up this lacuna.

Oaks play an important role in the forestry practices within Europe (Rock et al. 2004) where in total 22 autochthonous oak species are known to occur (Tutin et al. 2001). In Central Europe, the Turkey oak Q. cerris ranks among the most important oak species along with Q. robur L. and Q. petraea (Matt.) Liebel. (Führer 1998). Besides the importance of Q. cerris as a forest tree of economic importance, this oak species has also been planted as an ornamental tree in urban areas (Kabiček 2017). Of oak species in this region, Q. cerris has the latest budburst (Goliašová & Michalková 2006) timed approximately two weeks later compared with other oak species (Patocka 1954; Schafellner et al. 2005). Quercus cerris has a wide distribution from South-Eastern Europe (optimum) to Central Europe (Goliašová & Michalková 2006).

Oak trees in Central Europe host over 300 lepidopteran species (Patocka 1954, 1980; Csóka & Szabóky 2005). Their larvae are important leaf consumers and key components of the tree-dwelling fauna. Many of them are polyphagous, causing damage to forest, fruit and ornamental trees. The highest number of moth larvae on oaks is recorded from mid-April until mid-June, that is, approximately 80–90% of the larvae associated with oaks are found within this period (Patocka 1954). The species assemblages dominated by the larvae of Operophthera brumata and Tortrix viridana (the “brumata-viridana complex”) occur first, being synchronized with the budburst of their hosts. Later on throughout the season, this species complex is followed by the larvae of Lymantria dispar, Archips xylosteana, Orthosia spp. etc. (the “dispar-xylosteana complex”). They feed on the young leaves of Q. cerris and fully developed leaves of other oak species (Patocka et al. 1999). It might seem that late flushing Q. cerris will host less moth species than other co-occurring oak species (Kulfan 1992, 2012; Csóka & Szabóky 2005).

Life histories and phenological synchrony between folivorous moth larvae and the budburst of their host plants have been studied mostly in abundant and economically important species such as O. brumata (Grison & Silvestre de Sacy 1954; Mrkva 1968; Edland 1971; Holliday 1977; Graf et al. 1995; Tikkanen & Julkunen-Titto 2003), Lymantria dispar (Schoff et al. 1999; Hunter & Elkinton 2000; Schafellner et al. 2005; Milanović et al. 2014), and T. viridana (Du Merle 1988; Ivashov et al. 2002; Tiberi et al. 2005). Not much is known about other moth species foraging on trees (Forkner et al. 2008).

To get more insights into the effect of budburst of oaks on the occurrence of their lepidopteran associates we investigated the complex of spring-feeding moth larvae developing on two co-occurring oak species with different budburst phenologies: (1) late flushing Q. cerris and (2) early flushing Q. pubescens. The species assemblages on these two oak species were constituted by O. brumata and T. viridana, the synchrony of which with their hosts is well known (T. viridana: Du Merle 1983; Du Merle & Mazet 1983; Tiberi et al. 2005; O. brumata: Van Dongen et al. 1997; Tikkanen & Lyttikäinen-Saarenmaa 2002), as well as many other species within the “brumata-viridana complex”.

We predicted that Q. cerris and Q. pubescens would host similar species assemblages, and that the abundance of moth larvae would be lower on Q. cerris because of later budburst. We compared (1) the species composition of moth larvae assemblages, (2) number of species and (3) abundance of predominant species and abundance of all species between mature and young Q. cerris and Q. pubescens trees co-occurring in the temperate oak forest in Central Europe.

**MATERIAL AND METHODS**

**Study area.** Study was carried out in the southern part of the Western Carpathians, in the Krupina planina plain in Slovakia, Central Europe (48°10′0.19″N, 18°59′46.08″E), at the altitude between 265 and 330 m a.s.l. The area belongs to a warm climatic region with mean annual air temperature 8–9°C and mean annual precipitation between 600 and 700 mm (Klimatický atlas Slovenska 2015). Data were collected in an open-canopy xeric thermophilous oak forest dominated by pubescent oak (Quercus pubescens) and Turkey oak (cerris). Other tree species such as Acer campestre L., A. tataricum L., Tilia spp., Sorbus terminalis (L.) Crantz., Crataegus spp.,
Carpinus betulus L., Pyrus spp., and Ulmus spp. were infrequent and less abundant.

Collecting moth larvae. Moth larvae were collected from Q. cerris and Q. pubescens trees during the first week of May 2015 and May 2016. They were obtained from oak branches (up to 3 m from the ground level in the case of mature trees and up to 2 m in the case of young trees) using beating trays with a diameter of 1.0 m (Basset et al. 1997). The larvae collected from three branches of one mature tree or from two branches from one young tree represented one sample. The samples were obtained from a total of 34 mature trees of each oak species in the first year, and from a total of 30 young trees (up to 2 m high) of each oak species growing solely in the forest understorey in the second year. Collected larvae were preserved in 75% ethanol and determined in the laboratory according to Patocka (1954, 1980), Wagner (2005), and Rennwald and Rodeland (2013). Moth assemblages on each oak species were characterised by the species richness, abundance, and dominance of abundance of recorded species. The larvae of A. marginaria and A. aurantiaria, which are difficult to distinguish by external characters (sibling species), were considered as a single taxon Agriopis spp. The nomenclature of the species follows Pastorášis et al. (2013).

Data analysis. The number of species and abundance of moth larvae were analysed using one-way analysis of deviance (ANODEV) models separately for mature and young Q. cerris and Q. pubescens. The negative binomial and Poisson error distributions with log-link were used to test the effect of tree species on the number of moth species and abundance of moth larvae. The number of species models was then verified in the rarefaction analysis using species accumulation curves and by bias-corrected abundance-based Chao index estimations of the lower bounds for the total number of species (Chiù et al. 2014). The rarefaction was based on Hurlbert’s formulation (Hurlbert 1971) with standard errors calculated according to Heck et al. (1975). The effects of the ANODEV models were tested using the PIT-trap resampling method (Warton et al. 2017).

The effect of mature and young trees of both Quercus species on the composition of species assemblages was tested by the permutational multivariate analysis of variance (perMANOVA; Anderson 2001). The species abundance data were log(x + 1) transformed and the Bray-Curtis dissimilarity index (Bray & Curtis 1957) was used in the perMANOVA. The tests were done using unrestricted permutation of residuals. Results of the perMANOVA models were presented using the nonmetric multidimensional scaling ordination method (NMDS; Kruskal 1964). The NMDS was run by the wrapper function metaMDS in the vegan package (Oksanen et al. 2017). The NMDS ordinations were extended using the indicator species analysis, and abundant species in assemblages were tested using the IndVal function (Dufrène & Legendre 1997). The results of the indicator species analysis were adjusted for multiple testing using Holm’s family-wise error rate method (Holm 1979).

The significance level of 0.05 was used. Statistical analyses and graphical outputs were made in R (R Core Team 2016) using the packages boot (Canty & Ripley 2016), indicspecies (De Cáceres & Legendre 2009), mvabund (Wang et al. 2017), and vegan (Oksanen et al. 2017).

RESULTS

Quercus cerris and Q. pubescens yielded in total 10 601 individuals of moth larvae of 53 species (Table 1). A total of 2 259 larvae and 40 species were recorded on Q. cerris, and a total of 8 042 larvae and 47 species were obtained from Q. pubescens (Table 1). As many as 35 species (66% of the recorded species), including all abundant species, occurred on both oak species. Species found on a single oak species were not abundant (D < 1.0%) (Table 1).

The composition of larval assemblages differed between Q. cerris and Q. pubescens in both mature (pseudo-F = 18.848, P = 0.0001; Figure 1A) and young trees (pseudo-F = 4.451, P < 0.0001; Figure 1B). Also, a comparison of assemblages using the quantitative and qualitative Sørensen indices (SI) calculated from the four pooled datasets (mature Q. cerris vs. mature Q. pubescens, young Q. cerris vs. young Q. pubescens) reflected differences between assemblages. Both similarity indices between the corresponding assemblages on Q. cerris and Q. pubescens varied from low to medium values (SI = 0.44–0.76).

The number of species was significantly lower in samples from Q. cerris than from Q. pubescens on both mature (P < 0.0001) and young trees (P < 0.001) (Figure 2). However, when considering the same number of larvae in the rarefaction analysis (Figure 3), the rarefied number of species was higher on mature Q. cerris than on mature Q. pubescens, although this was negligible (P > 0.05). The estimation for
Table 1. Dominance of abundance (%) of moth species on mature and young *Quercus cerris* (Qc) and *Quercus pubescens* (Qp) in the temperate forest in Central Europe. Dominant species (dominance > 5.0%) are highlighted

<table>
<thead>
<tr>
<th>Species</th>
<th>Mature Qc</th>
<th>Mature Qp</th>
<th>Young Qc</th>
<th>Young Qp</th>
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</thead>
<tbody>
<tr>
<td>Psychidae</td>
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<tr>
<td>Psychidae 1</td>
<td>&lt; 1.0</td>
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<td>Psychidae 2</td>
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<td>Ypsolophidae</td>
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<tr>
<td><em>Ypsolopa asperella</em> (Linnaeus, 1761)</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Ypsolopa lucella</em> (Fabricius, 1775)</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Ypsolopa alpella</em> (Denis et Schiffermüller, 1775)</td>
<td>&lt; 1.0</td>
<td>&lt; 1.0</td>
<td>&gt; 1.0</td>
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<tr>
<td><em>Ypsolopa sylvella</em> (Linnaeus, 1767)</td>
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<td><em>Ypsolopa ustella</em> (Clerck, 1759)</td>
<td>&lt; 1.0</td>
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<td>Chimabachidae</td>
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<tr>
<td><em>Dasystoma salicella</em> (Hübner, 1796)</td>
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<td><em>Psoricoptela gibbosella</em> (Zeller, 1839)</td>
<td>&lt; 1.0</td>
<td>&lt; 1.0</td>
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<td><em>Anacampsis timidella</em> (Woek, 1887)</td>
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<td>0</td>
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<td>&lt; 1.0</td>
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<tr>
<td>Tortricidae</td>
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<tr>
<td><em>Tortrix viridana</em> (Linnaeus, 1758)</td>
<td>&lt; 1.0</td>
<td>2.63</td>
<td>2.48</td>
<td>6.38</td>
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<tr>
<td><em>Aleimma loeflingiana</em> (Linnaeus, 1758)</td>
<td>0</td>
<td>&lt; 1.0</td>
<td>&lt; 1.0</td>
<td>1.65</td>
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<tr>
<td><em>Tortricodes alternella</em> (Denis et Schiffermüller, 1775)</td>
<td>&lt; 1.0</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Eudemis profundana</em> (Denis et Schiffermüller, 1775)</td>
<td>0</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Zeiraphera isertana</em> (Fabricius, 1794)</td>
<td>&lt; 1.0</td>
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<tr>
<td>Lycaenidae</td>
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<td><em>Favonius quercus</em> (Linnaeus, 1758)</td>
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<td>&lt; 1.0</td>
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<tr>
<td><em>Satyrium ilicis</em> (Esper, 1779)</td>
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<td>0</td>
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<td>&lt; 1.0</td>
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<tr>
<td>Pyralidae</td>
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<tr>
<td><em>Phycita roborella</em> (Denis et Schiffermüller, 1775)</td>
<td>&lt; 1.0</td>
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<td>Drepanidae</td>
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<tr>
<td><em>Cymatophorina diluta</em> (Denis et Schiffermüller, 1775)</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Polyploca ridens</em> (Fabricius, 1787)</td>
<td>&lt; 1.0</td>
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<td><em>Asphalia ruficollis</em> (Fabricius, 1787)</td>
<td>&lt; 1.0</td>
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<td>&lt; 1.0</td>
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<tr>
<td>Geometridae</td>
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<tr>
<td><em>Alsophila aescularia</em> (Denis et Schiffermüller, 1775)</td>
<td>&lt; 1.0</td>
<td>&lt; 1.0</td>
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<td>&lt; 1.0</td>
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<tr>
<td><em>Alsophila aceraria</em> (Denis et Schiffermüller, 1775)</td>
<td>0</td>
<td>&lt; 1.0</td>
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<td>&lt; 1.0</td>
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<tr>
<td><em>Apoechima hispidaria</em> (Denis et Schiffermüller, 1775)</td>
<td>4.29</td>
<td>1.61</td>
<td>1.86</td>
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<tr>
<td><em>Phigalia pilosaria</em> (Denis et Schiffermüller, 1775)</td>
<td>&lt; 1.0</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Lycia pomonaria</em> (Hübner, 1790)</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Biston strataria</em> (Hufnagel, 1676)</td>
<td>0</td>
<td>&lt; 1.0</td>
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</tr>
<tr>
<td><em>Agriopis leucophaearia</em> (Denis et Schiffermüller, 1775)</td>
<td>83.00</td>
<td>79.10</td>
<td>81.57</td>
<td>68.48</td>
</tr>
<tr>
<td><em>Agriopis bajaria</em> (Denis et Schiffermüller, 1775)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Agriopis spp. = A. aurantiaria</em> (Hübner, 1799) + <em>A. marginaria</em> (Fabricius, 1776)</td>
<td>2.70</td>
<td>1.60</td>
<td>1.66</td>
<td>2.13</td>
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<tr>
<td><em>Erannis defoliaria</em> (Clerck, 1759)</td>
<td>1.16</td>
<td>1.38</td>
<td>1.04</td>
<td>1.06</td>
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<td><em>Colotois pennaaria</em> (Linnaeus, 1761)</td>
<td>&lt; 1.0</td>
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<tr>
<td><em>Chloroclysta sitara</em> (Hufnagel, 1676)</td>
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<td>&lt; 1.0</td>
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</table>
2000 larvae, for example, predicted the occurrence of 32.6 ± 0.7 species on mature *Q. cerris* and 30.5 ± 2.2 species on mature *Q. pubescens* (Figure 3A). The Chao index estimated the occurrence of 49.5 ± 12.8 species on mature *Q. cerris* and 48.0 ± 6.6 species on mature *Q. pubescens*. In the case of young trees, the estimations for e.g. 450 individuals gave fewer species on *Q. cerris* (20.6 ± 1.0 species) than on *Q. pubescens* (25.3 ± 1.8 species) (Figure 3B), and the Chao index, in agreement, predicted much fewer species on *Q. cerris* and *Q. pubescens*.
species on young *Q. cerris* (23.1 ± 2.5) than on young *Q. pubescens* (38.2 ± 6.4 species).

The larvae of *A. leucophaearia*, *O. brumata* and *T. viridana* constituted more than 85% of the larvae recorded on each oak species and in each age category (Table 1). The larvae of *A. leucophaearia* dominated considerably (dominance between 68 and 83%; Table 1) and consistently on both young and mature trees of both oak species, whereas *O. brumata* dominated (dominance > 5.0%) all assemblages except for the assemblage hosted by mature *Q. cerris*. *Tortrix viridana* dominated only on young *Q. pubescens* (Table 1).

On mature trees, the abundance of *A. leucophaearia* was 3.3, of *O. brumata* 11.4, and of *T. viridana* 21.0 times lower on *Q. cerris* than on *Q. pubescens* (all three species, *P* < 0.0001). On young trees, the abundance of *A. leucophaearia* was 1.5, abundance of *O. brumata* 4.2 and abundance of *T. viridana* 4.5 times lower on *Q. cerris*. These differences were significant (*P* < 0.0001) except for the case of *A. leucophaearia* (*P* = 0.129).

The total number of moth larvae in assemblages was approximately 3.5 times lower on mature (*P* < 0.0001) and almost twice lower on young *Q. cerris* (*P* = 0.013) in comparison with the corresponding numbers on *Q. pubescens* (Figure 4).

Five indicator species specialised on certain hosts were documented. The larvae of *Catocala nympha-goga* showed affinity (IndVal = 0.45, *P* = 0.0001) to mature *Q. cerris*, and none of the species preferred young *Q. cerris*. The larvae of *A. leucophaearia* (In-
dVal = 0.77, \( P = 0.0001 \), \textit{E. defoliaria} (IndVal = 0.73, \( P = 0.0001 \)) and \textit{T. viridana} (IndVal = 0.84, \( P = 0.0001 \)) preferred mature \textit{Q. pubescens}, while those of \textit{O. brumata} showed affinity to both mature (IndVal = 0.89, \( P = 0.0001 \)) and young \textit{Q. pubescens} (IndVal = 0.70, \( P = 0.0001 \)).

**DISCUSSION**

Our data suggest species-rich ephemeral assemblages of moth larvae of the “brumata-viridana complex” on both early flushing \textit{Q. pubescens} and late flushing \textit{Q. cerris}. All moth species found on \textit{Q. cerris} and \textit{Q. pubescens} are known to develop on oaks (Csóka & Szabóky 2005; Patočka & Kulfan 2009). The recorded larval assemblages included characteristic species of the “brumata-viridana complex” (Patočka et al. 1999). Besides the well-known pests such as \textit{O. brumata} and \textit{T. viridana} also other accompanying species can contribute significantly to the defoliation of host trees (Patočka 1954; Schwenke 1978; Patočka et al. 1999).

The same abundant species were present in all assemblages. However, similarity between the larval assemblages on \textit{Q. cerris} and \textit{Q. pubescens} was relatively low, reflecting differences in assemblage composition (especially in the presence/absence of not abundant species and abundance of species).

The lower number of larvae on \textit{Q. cerris} than on \textit{Q. pubescens} obtained by the same sampling effort (from the same number of sample branches) reflected the lower number of moth species. This may explain the lower number of moth species on late flushing \textit{Q. cerris} compared with early flushing oaks also mentioned in other studies (e.g. Kulfan 1992, 2012; Csóka & Szabóky 2005). Our results suggest that the same number of larvae on mature oak trees of both species provides a similar number of species.

The most important results of our study relate to the lower number of all moth larvae in assemblages and the lower abundance of dominant species (\textit{A. leucophaearia}, \textit{O. brumata}, and \textit{T. viridana}) on \textit{Q. cerris} than on \textit{Q. pubescens}. This suggests a similar response of the species of the “brumata-viridana complex” to asynchrony between the hatching of larvae and the budburst of \textit{Q. cerris} trees.

The females of \textit{O. brumata} and \textit{T. viridana} do not prefer any host tree for oviposition (Grison & Silvestre de Sacy 1954; Graf et al. 1995; Tiberi et al. 2005). Therefore, \textit{Q. cerris} and \textit{Q. pubescens} trees co-occurring in a forest may have an equal chance to be infested by these moth species and, possibly, by other species within the “brumata-viridana complex”. Besides the density and distribution of eggs, the occurrence of moth larvae in forest canopies strongly depends on their dispersal ability and mortality (Holliday 1977; Tiberi et al. 2005). When the larvae of the “brumata-viridana complex” are hatching, conditions in the crowns of \textit{Q. cerris} differ from those in the crowns of \textit{Q. pubescens}. As the buds of \textit{Q. cerris} are still closed, there is no food available for moth larvae. The neonate larvae of \textit{O. brumata} and \textit{T. viridana} and many other species also require opening buds as a shelter (Patočka 1954; Schwenke 1978; Tiberi et al. 2005). When present on \textit{Q. cerris} with the late budburst, young larvae cannot find any food and shelter (Zalucki et al. 2002). Moreover,
compared with *Q. pubescens*, the larvae on the nude branches of *Q. cerris* are more exposed to biotic (natural enemies) and abiotic factors (temperature fluctuation, UVB and infrared radiation, rain, etc.) (cf. Damman 1987; Kamata & Igarashi 1994; Buck & Callaghan 1999; Zalucki et al. 2002; Pincebourde et al. 2007; Abarca et al. 2014) which may affect their occurrence on trees.

Starving young moth larvae die or disperse to find appropriate food. They can balloon on wind currents (Edland 1971; Holliday 1977; Schwenke 1978) or they can lower down the tree (Mrkva 1968). The rate of dispersal depends on the ability of larvae to withstand starvation. For example, while young larvae of *O. brumata* can live without feeding up to 4–5 days only (Cuming 1961; Wint 1983), those of *T. viridana* can withstand starvation up to 12 days (Hunter 1990). The larvae of the latter species are then less inclined to disperse (Mrkva 1968; Hunter 1990). In temperate oak forests, *Q. cerris* can be colonised by the larvae dispersing from *Q. pubescens*, when open buds or leaves are available. As our results suggest, the dispersal of *O. brumata* from *Q. pubescens* to *Q. cerris* trees can be more pronounced than that of *T. viridana*.

The intraspecific variation in the date of larval hatching and the budburst of the hosts causes that some larvae of the same population can find appropriate food resources while the other larvae cannot detect them (Du Merle 1988; Tikkanen & Julkunen-Titto 2003). In the case of *Q. cerris* with the late budburst, the moth larvae which hatched later may take advantage over those hatched sooner.

Global climate change influences the phenology of both insect herbivores and their hosts but not at the same rates. This may lead to asynchrony between the phenology of moths and their hosts, resulting in only slight damage to foliage (van Asch & Visser 2007). According to van Asch et al. (2007), over the last two decades, the egg hatching date of *O. brumata* advanced more than the date of *Q. robur* budburst. Such observations suggest that a relatively narrow time span between the hatching of this moth and the flushing of *Q. cerris* trees gets wider.

According to the theory of adaptive deme formation (Edmunds & Alstad 1978; Van Dongen et al. 1997), some populations of herbivorous Lepidoptera have adapted genetically to an individual host tree and the phenology of its budburst (Tikkanen & Lyytikäinen-Saarenmaa 2002; van Asch et al. 2013). In forests, where trees of different species often grow relatively close to each other, moth adults and larvae can migrate among them. Therefore, the hybridisation of individuals developing on different trees acts against the establishment of specialised populations adapted to the phenology of individual trees or tree species (Tikkanen & Julkunen-Titto 2003). The presence of early flushing *Q. pubescens* or other tree species with early budburst in the stands of *Q. cerris* may prevent or eliminate the occurrence of specific moth populations adapted to late flushing trees.

The geometrid *A. leucophaearia* was the most abundant species which consistently prevailed on both oak species irrespective of the age of infested oak trees. Its larvae feed on broadleaved trees preferring *Quercus* spp. (Patočka 1954; Ebert et al. 2003; Patočka & Kulfan 2009). In Central Europe they hatch over a longer time period than those of *O. brumata*, hence, different instars co-occur at the same time (J. Kulfan, personal observation). The larvae which hatch later can then find open buds of *Q. cerris* trees with ease. This could explain the relatively high abundance of this species even on *Q. cerris*. The high abundance of *A. leucophaearia* suggests the economic importance of this previously overlooked pest of oak trees, the larvae of which can be misidentified with those of *O. brumata*. At the present moment we do not know much about the phenological synchrony of *A. leucophaearia* with its hosts. We suppose that this species should be paid greater attention from a forestry point of view because it can cause severe defoliation in oak forests.

*Catocala nymphagoga* was considered the only indicator species on mature *Q. cerris*. This thermophilous species is abundant in the Mediterranean and Submediterranean oak forests (Goater et al. 2003) but also occurs in the temperate forests of Central Europe (Patočka 1954; Nowacki et al. 2003; Macek et al. 2008; Nowacki & Wasała 2008). It is a southern species, the life cycle and phenology of which could differ between Central and southern Europe. Hence, *Q. cerris* with late budburst could be more appropriate for the larvae of *C. nymphagoga* feeding on various oak species within Europe (Ahola & Silvonen 2005; Csóka & Szabóky 2005; Patočka & Kulfan 2009).

Considering the low numbers of moth larvae of the “brumata-viridana complex” on late flushing *Q. cerris* it is evident that the late budburst is among important defence mechanisms of plants against the attack by herbivores (cf. Wesołowski & Rowiński 2008). Knowledge of the phenology of *Q. cerris* and other late flushing tree species can be applied in
silvicultural and horticultural practices aimed to protect and maintain forest, fruit and ornamental tree species. Herein, the emphasis was placed on the moth larvae within the "brumata-viridana complex". The late occurring spring larvae within the "dispar-xylotreana complex" take advantage of consuming high-quality leaves of late flushing tree species such as Q. ceras. Lymantria dispar, an important defoliator of oak trees within Europe, can be a good example of such species (cf. Schwenke 1978; Milanović et al. 2014). However, in the further future the abundance of this outbreak species could be lowered by the exotic entomopathogenic fungus Entomophaga maimaiga (Zúbrik et al. 2016).

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