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

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Abstract

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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 pubescen*s; 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-Tiitto 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-Tiitto

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 & Rowiński 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 (Kabíček 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 (Patočka 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 (Patočka 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 (Patočka 1954). The species assemblages dominated by the larvae of *Operophtera 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 (Patočka *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-Tiitto 2003), *Lymantria dispar* (Schopf *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 & Lyytikäinen-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 Krupinská 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 torminalis* (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 Patočka (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 Pastorális *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 (Chiu *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 meta-MDS 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 (Dufrêne & 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 2 559 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. pubescenss*, 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

Species	Mature Qc	Mature Qp	Young Qc	Young Qp
Psychidae				
Psychidae 1	< 1.0	0	0	0
Psychidae 2	< 1.0	0	0	0
Ypsolophidae				
Ypsolopha asperella (Linnaeus, 1761)	< 1.0	< 1.0	0	0
Ypsolopha lucella (Fabricius, 1775)	< 1.0	< 1.0	0	< 1.0
Ypsolopha alpella (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	< 1.0	< 1.0
Ypsolopha sylvella (Linnaeus, 1767)	< 1.0	0	0	0
Ypsolopha ustella (Clerck, 1759)	< 1.0	< 1.0	0	0
Chimabachidae				
Dasystoma salicella (Hübner, 1796)	0	< 1.0	0	0
Gelechiidae				
Psoricoptela gibbosella (Zeller, 1839)	< 1.0	< 1.0	0	0
Anacampsis timidella (Wocke, 1887)	0	0	0	< 1.0
Tortricidae				
Tortrix viridana (Linnaeus, 1758)	< 1.0	2.63	2.48	**6.38**
Aleimma loeflingiana (Linnaeus, 1758)	0	< 1.0	< 1.0	1.65
Tortricodes alternella (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	< 1.0	0
Eudemis profundana (Denis et Schiffermüller, 1775)	0	< 1.0	0	0
Zeiraphera isertana (Fabricius, 1794)	< 1.0	< 1.0	0	< 1.0
Lycaenidae				
Favonius quercus (Linnaeus, 1758)	0	< 1,0	0	0
Satyrium ilicis (Esper, 1779)	0	0	0	< 1.0
Pyralidae				
Phycita roborella (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	< 1.0
Drepanidae				
Cymatophorina diluta (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	< 1.0
Polyploca ridens (Fabricius, 1787)	< 1.0	< 1.0	< 1.0	0
Asphalia ruficollis (Fabricius, 1787)	< 1.0	< 1.0	< 1.0	< 1.0
Geometridae				
Alsophila aescularia (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	< 1.0
Alsophila aceraria (Denis et Schiffermüller, 1775)	0	< 1.0	< 1.0	< 1.0
Apocheima hispidaria (Denis et Schiffermüller, 1775)	4.29	1.61	1.86	< 1.0
Phigalia pilosaria (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	0
Lycia pomonaria (Hübner, 1790)	< 1.0	< 1.0	0	0
Biston strataria (Hufnagel, 1767)	0	< 1.0	0	0
Agriopis leucophaearia (Denis et Schiffermüller, 1775)	**83.00**	**79.10**	**81.57**	**68.48**
Agriopis bajaria (Denis et Schiffermüller, 1775)	0	0	0	< 1.0
Agriopis spp. = *A. aurantiaria* (Hübner, 1799) + *A. marginaria* (Fabricius, 1776)	2.70	1.60	1.66	2.13
Erannis defoliaria (Clerck, 1759)	1.16	1.38	1.04	1.06
Colotois pennaria (Linnaeus, 1761)	< 1.0	0	0	0
Chloroclysta siterata (Hufnagel, 1767)	0	< 1.0	0	0

Table 1 to be continued

Species	Mature Qc	Mature Qp	Young Qc	Young Qp
Operophtera brumata (Linnaeus, 1758)	**3.08**	**10.17**	**5.18**	**12.28**
Erebidae				
Lymantria dispar (Linnaeus, 1758)	< 1.0	< 1.0	< 1.0	< 1.0
Ocneria rubea (Denis et Schiffermüller, 1775)	0	0	0	< 1.0
Eilema complana (Linnaeus, 1758)	0	< 1.0	0	0
Callimorpha dominula (Linnaeus, 1758)	0	0	< 1.0	0
Catocala nymphagoga (Esper, 1787)	1.35	< 1.0	< 1.0	< 1.0
Noctuidae				
Asteroscopus sphinx (Hufnagel, 1766)	0	< 1.0	< 1.0	< 1.0
Conistra vaccinii (Linnaeus, 1761)	0	< 1.0	1.04	< 1.0
Jodia croceago (Denis et Schiffermüller, 1775)	0	0	0	< 1.0
Dicycla oo (Linnaeus, 1758)	0	< 1.0	< 1.0	< 1.0
Rileyiana fovea (Treitschke, 1825)	0	< 1.0	0	0
Scotochrosta pulla (Denis et Schiffermüller, 1775)	0	< 1.0	0	0
Dryobotodes eremita (Fabricius, 1775)	< 1.0	< 1.0	< 1.0	< 1.0
Dryobotodes monochroma (Esper, 1790)	< 1.0	0	< 1.0	0
Orthosia incerta (Hufnagel, 1766)	< 1.0	< 1.0	0	< 1.0
Orthosia miniosa (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	< 1.0
Orthosia cerasi (Fabricius, 1775)	< 1.0	< 1.0	< 1.0	< 1.0
Orthosia cruda (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	< 1.0
Anorthoa munda (Denis et Schiffermüller, 1775)	< 1.0	< 1.0	0	< 1.0
Number of individuals	2 076	7 195	483	847
Number of species	34	42	22	32

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 ± 0.6 species) than on *Q. pubescens* (25.3 ± 1.8 species) (Figure 3B), and the Chao index, in agreement, predicted much fewer
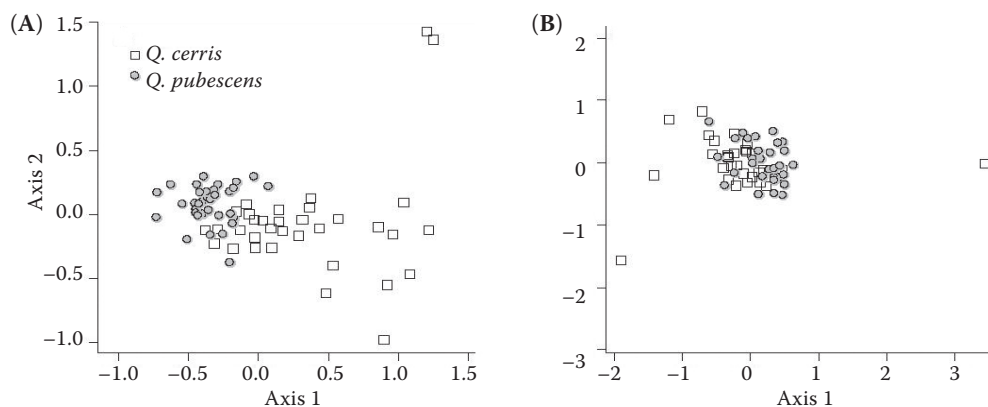

Figure 1. Nonmetric multidimensional scaling of species assemblages on mature (**A**) and young (**B**) *Quercus cerris* and *Quercus pubescens* in the temperate forest in Central Europe

The Bray-Curtis dissimilarity index was used as a measure contrasting species assemblages; stress values of the ordination configuration in the two dimensions were 0.13 in mature and 0.14 in young trees
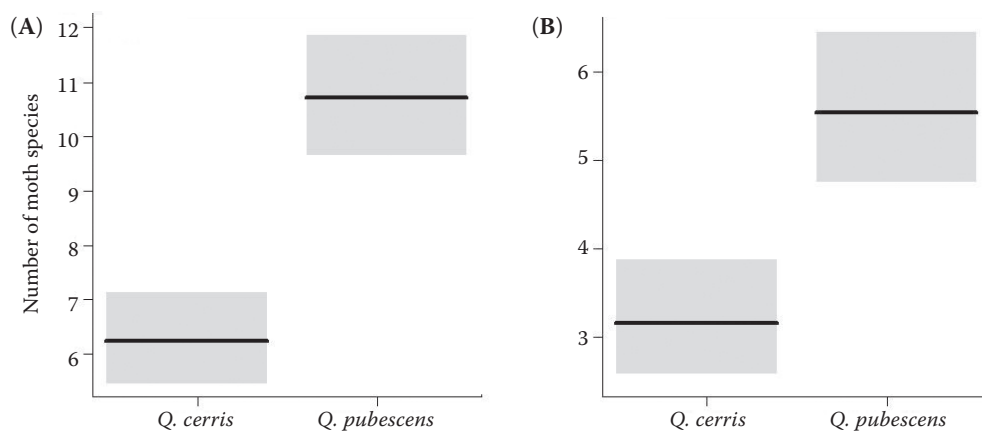
Figure 2. Number of moth species in samples from mature (**A**) and young (**B**) *Quercus cerris* and *Quercus pubescens* trees in the temperate forest in Central Europe

Horizontal lines denote the mean, bars denote the 95% confidence intervals

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 nymphagoga* 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-
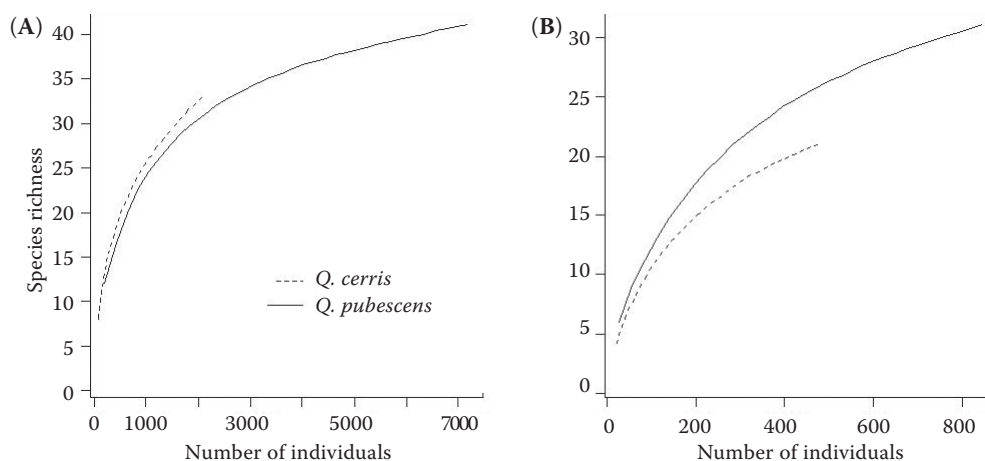

Figure 3. Expected species richness in relation to the number of collected moth larvae – rarefied number of moth species on mature (**A**) and young (**B**) *Quercus cerris* and *Quercus pubescens* trees in the temperate forest in Central Europe

The larvae were obtained from a total of 102 branches of 34 mature trees and from a total of 60 branches of 30 young trees of each oak species
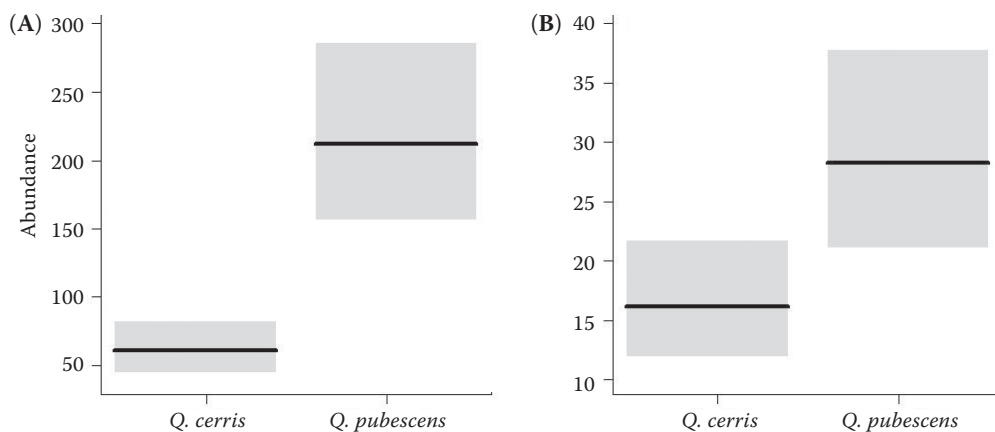
Figure 4. Abundance of moth larvae on mature (**A**) and young (**B**) *Quercus cerris* and *Quercus pubescens* trees in the temperate forest in Central Europe

Horizontal lines denote the mean, bars denote the 95% confidence intervals

dVal = 0.77, *P* = 0.0001), *E. defoliaria* (IndVal = 0.73, *P* = 0.0001) and *T. viridana* (IndVal = 0.84, *P* = 0.0001) preferred mature *Q. pubescens*, while those of *O. brumata* showed affinity to both mature (IndVal = 0.89, *P* = 0.0001) and young *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 *Q. pubescens* and late flushing *Q. cerris*. All moth species found on *Q. cerris* and *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 *O. brumata* and *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 *Q. cerris* and *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 *Q. cerris* than on *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 *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 (*A. leucophaearia*, *O. brumata*, and *T. viridana*) on *Q. cerris* than on *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 *Q. cerris* trees.

The females of *O. brumata* and *T. viridana* do not prefer any host tree for oviposition (Grison & Silvestre de Sacy 1954; Graf *et al.* 1995; Tiberi *et al.* 2005). Therefore, *Q. cerris* and *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 *Q. cerris* differ from those in the crowns of *Q. pubescens*. As the buds of *Q. cerris* are still closed, there is no food available for moth larvae. The neonate larvae of *O. brumata* and *T. viridana* and many other species also require opening buds as a shelter (Patočka 1954; Schwenke 1978; Tiberi *et al.* 2005). When present on *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-Tiitto 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-Tiitto 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 & Wasąla 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-xylosteana complex" take advantage of consuming high-quality leaves of late flushing tree species such as *Q. cerris*. *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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