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## Species composition of arthropods on six understory plant species growing in high and low light conditions

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**Abstract:** The quality of leaves as food for insects is affected both by plant species and the light conditions present during growth. Little information exists concerning the impact of these factors on the diversity of insects that live in the forest understory. We studied arthropod fauna on six understory plant species commonly occurring in Europe. Different groups of herbivorous insects were identified, as well as predatory insects and arachnids. We analysed the influence of both plant species and light conditions during growth (low light; high light) on the species spectrum, and the number of insect specimens present. The resulting data were investigated in relation to the susceptibility of plant leaves to feeding by folivorous insects, as determined in earlier studies. We compared the similarity in species diversity, based on the Sørensen's coefficient, and discussed the potential causes of observed differences in leaf damages. We found a total of 153 arthropod taxa on studied plants, under both light conditions. *Corylus avellana* and *Prunus serotina*, species characterized by greater leaf damage, have a wider diversity of arthropod species, and a greater number of herbivorous insects. Generally, light conditions had a greater effect on arthropod abundance than on species diversity. For two plant species, *C. avellana* and *P. serotina*, light conditions strongly, but reversely, influenced the total number of insects and, thus, the extent of leaf damage. The number and abundance of zoophagous species, and ratio to folivores (except *C. avellana*) are associated more with plant species than with light conditions.

**Keywords:** *Cornus sanguinea, Corylus avellane, Frangula alnus, Prunus padus, Prunus serotina, Sambucus nigra*

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## Introduction

Forests in Europe are mainly single-species (Spiecker, 2003) in most cases consisting of conifers such as pine (Mason & Alía, 2000) and spruce (Klimo et al., 2000). From the point of view of the ecological stability of the stand and forest management, single-crop cultivation is a negative phenomenon, favouring pest gradations, among other issues. These gradations can be counteracted by introducing understory species (e.g. shrubs or low-level trees) that, even with limited access to light, remain in the undergrowth layer (Szczygiel et al., 2008). This is a natural method of forest protection, reducing the problems associated with the mass appearance of insects in monoculture stands. The possibility of introducing shrubs into the understory depends on whether the habitat conditions of the stand adequately meet the requirements of individual species. This in turn determines the diversity of herbivorous insects and their enemies – zoophages (predatory arthropods and parasites) – that can be found in such a stand.

Most researchers consider that the food preferences of folivores, and thus the extent of damage caused by insects (e.g. perforation of plant leaves), are mainly determined by the chemical composition of the leaves, which is dependent on the species (Sharov et al., 1999; Hunter, 2001; Uusitalo, 2004). Studies of herbivorous species, which are less common and typically cover a narrower scope than those concerning zoophages, generally concern the occurrence, morphology and biology of insects on forest tree species. Insect pests of understory plant species have garnered much less attention. Studies investigating such pests are usually limited to establishing a species checklist, and describing the main pest or mentioning the folivorous species most often found on a given species of shrub. In the case of European shrubs, most studies related to the presence of herbivores and the damage they cause have involved common hazel, *Corylus avellana* L. (Axelsson et al., 1973; Olivero et al., 2003). This is because of the great economic importance of *C. avellana*, as hazelnuts are used in both the food and pharmaceutical industries. Due to the widespread use of hazel crops, the species composition of herbivorous species has been analysed not only under natural conditions, but also in plantation crops (Gantner & Jaśkiewicz, 2002). Such research mainly concerns the identification of insects in periods when gradation occurs, methods for their eradication and assessment of the degree of damage they inflict on the fruiting of shrubs.

Due to the prevalence of European bird cherry (*Prunus padus* L.) in European forests, slightly more entomological research has been devoted to this species of shrub (Leather, 1985, 1994; Kooi et al., 1991; Alonso et al., 2000). Moreover, the intended

introduction of black cherry (*Prunus serotina* Ehrh.), and the negative consequences resulting from its expansiveness (Vanhellemont et al., 2009), has caused interest in the use of this alien species by native European herbivores (Karolewski et al., 2014, 2017; Vanhellemont et al., 2014; Mađerek et al., 2015). An additional cause for undertaking such research has been an attempt to explain the extremely high level of leaf damage caused by folivores of *P. padus* (Leather, 1986; Leather & Mackenzie, 1994; Alonso, 1999), as well as on *P. serotina* growing in the shade – much greater damage than observed for other species of understory shrubs (Karolewski et al., 2013).

Some attention has been devoted to research related to herbivores on the glossy buckthorn (*Frangula alnus* Mill.), as *F. alnus* is an alien and invasive species in North America, like *P. serotina* in Europe. Many species of insects found on *F. alnus* have been identified in studies carried out in Eastern Austria, Germany and Switzerland (Malicky et al., 1970). Even more extensive research, involving as many as 99 sites in Europe, was carried out by Gassmann et al. (Gassmann et al., 2008), who additionally compared their results with those obtained by previously mentioned authors.

The occurrence of herbivores on the other two species of shrubs examined in this study has received less attention. In the case of common dogwood (*Cornus sanguinea* L.), attention should be paid to studies in which the authors provide, in addition to a folivorous species checklist, a description of the effect of stage of leaf development on feeding larvae of several species of insects (Jackson et al., 1999). Research carried out by Duffey et al. (Duffey et al., 1974) indicated that, relative to other understory species studied by the authors, the number of herbivorous species occurring on *C. sanguinea* was very small. Their results and our observations (Karolewski et al., 2013) indicate that in *C. sanguinea*, the damage caused by folivores is very small. There is also little information regarding insects feeding on the leaves of European elder (*Sambucus nigra* L.). Both the diversity and abundance of these insect species are small, and thus damage to the leaves of *S. nigra* is also rarely observed (Duffey et al., 1974; Atkinson & Atkinson, 2002).

The results of most studies indicate that the amount of damage caused by folivorous insects depends mainly on the species of plant. Occasionally, however, the light conditions during plant growth have a greater effect on insect damage than does plant species. The reason for this is that in some plant species, the light conditions strongly affect the structure of the leaves, both morphology and anatomy (Saldaña et al., 2005; Mađerek et al., 2017; Jagiełło et al., 2019), making the leaves easier or more difficult for folivores to bite. Leaves experiencing

greater insolation contain greater levels of secondary metabolites, which have important defence functions against herbivores (Jansen & Stamp, 1997; Henriksson et al., 2003). This has been confirmed by both field studies (Moreau et al., 2003; Ballaré et al., 2012) and experiments under controlled conditions (Fortin & Mauffette, 2002). The influence of light on leaf damage caused by folivorous insects can be indirect, through the structure and chemistry of leaves, or direct, by affecting insect fitness and behaviour. There is no one pattern – it varies from species to species and interactions between species and light may also occur (Karolewski et al., 2013; Łukowski et al., 2014; Łukowski et al., 2015b).

In our earlier studies, we reported large differences among six species of understory shrubs regarding leaf damage (perforation) due to insect feeding (Karolewski et al., 2013). By determining the impact on each species separately, we divided the examined shrub species into three groups: weakly damaged – *C. sanguinea*, *S. nigra* and *F. alnus*; moderately damaged – *P. serotina* and *C. avellana*; and strongly damaged – *P. padus*. In some species of plants, however, light had a strong effect on damage. In both plant species generally defined as moderately damaged, we observed large differences in leaf damage between plants growing in low light (LL) and high light conditions (HL). Most species growing in LL are characterised by greater susceptibility to folivore feeding than those growing in HL (Henriksson et al., 2003; Ingersoll et al., 2010; Calder et al., 2011). One such species is *P. serotina*. When growing in LL, the leaves of *P. serotina* show insect damage similar to that observed in the most damaged *P. padus*, whereas the leaves of *P. serotina* growing in HL show insignificant damage. In *C. avellana*, however, light conditions affect the magnitude of damage caused by folivores in a rather different manner than that observed in *P. serotina* and most other plant species. The leaves of *C. avellana* shrubs growing in HL are much more damaged than those growing in LL (Łukowski et al., 2015a). In turn, two other species (*C. sanguinea* and *S. nigra*) are characterised by weak damage to their leaves independent of the light conditions in which they grow. In *P. padus*, light conditions only slightly affect the magnitude of folivore damage, with damage in both LL and HL being very high. In the abovementioned studies (Karolewski et al., 2013), determination of defence compounds (soluble phenols and condensed tannins) and the main attractant (nonstructural carbohydrates and nitrogen) did not fully explain the differences in susceptibility to folivore feeding observed among plant species or among light conditions. The examples described above concerned only the relationships between plant species, light conditions and the degree of leaf damage (loss of surface area or leaf mass due to feeding of folivores). We therefore

assumed that it would be helpful to determine and compare the species composition and abundance of both herbivorous and zoophagous species present on these shrubs.

In research investigating the factors affecting the degree of leaf damage by folivores, relatively small attention has been given to the interaction of herbivorous insects with predatory organisms (Bergelson & Lawton, 1988; Björkman et al., 1997). Determining the quantitative relationship between folivores and their enemies/predators is useful for a more complete understanding of variation in the magnitude of leaf damage caused by folivores among plant species and light conditions for growth.

The main objective of the research presented here was to determine the species diversity and abundance of both herbivorous insects feeding on understory plant species and their natural enemies – zoophages. Light conditions have a significant impact on the structure and chemistry of leaves (Karolewski et al., 2013; Jagiełło et al., 2019) and, thus, their quality as food, which can impact the growth and development of herbivorous insects (Mađerek et al., 2015; Łukowski et al., 2015b). This, in turn, is closely related to the species composition and abundance of these herbivorous insects. Thus, when analysing species composition and abundance in the present study, the influence of the light conditions in which plants grow was also taken into account in addition to host plant species. Considering the above statements and having determined the species composition of insects present on the examined species of plants growing in different light conditions, we decided to answer the following questions: (1) do plant species exhibiting similar leaf damage by herbivores have similar species diversity and abundance of herbivores?; (2) do light conditions have a greater impact on the abundance of folivores or on their species diversity?; (3) whether plants weakly damaged by insects owe this to the wide species diversity and/or large abundance of zoophages?; and (4) whether occurrence of predatory arthropods is associated more strongly with plant species than with light conditions?

## Materials and Methods

### Plant material

Our study was conducted at the experimental forest of the Institute of Dendrology in Kórnik, Poland (52°14'N, 17°05'E; 75 m altitude), from April to October 2006 in order to take into account important growth and development phases (flowering, bud break, fruiting, etc.). Six forest understory plant species were used: European elder (*Sambucus nigra*

L.), black cherry (*Prunus serotina* Ehrh.), European bird cherry (*Prunus padus* L.), common dogwood (*Cornus sanguinea* L.), glossy buckthorn (*Frangula alnus* Mill.) and common hazel (*Corylus avellana* L.). Six adult individuals were selected of each species, with three plants (shrubs of 3–5 m high) growing under high light conditions (HL) – near the edges of wider forest roads or the edges of forest meadows – and the other three growing in low light conditions (LL; ca. 15–30% full light, when measured with an FF01 phytophotometer [Sonopan, Białystok, Poland] in clear weather in June between 13:00 and 14:00 hours), under the canopy of trees. All studied plants grew in a similar habitat, under a canopy of *Pinus sylvestris* L. with admixture of *Quercus robur* L., *Fagus sylvatica* L., *Carpinus betulus* L. and *Ulmus laevis* Pall. In the case of plants selected for research, there were no differences between density of the studied shrubs species. The studied plants did not grow individually, but in groups of several plants of a given species. The light conditions for leaf growth were characterised by a specific leaf area (SLA, cm<sup>2</sup> g<sup>-1</sup>). In each plant specimen, four samples were harvested (north, east, south, west) at a height of approx. 1.2 m from the ends of branches (10 leaves each sample = 40 leaves), and the average of each specimen was treated as a repeat (n = 3/treatment). The leaves were scanned and the surface of their projection was measured using the WinFOLIA program (version 2003b, Regent Instruments Inc., Quebec, Canada, [www.regentinstruments.com/](http://www.regentinstruments.com/)). The leaves were then dried at 65 °C in a forced air oven (ULE 600, Memmert GmbH + Co. KG, Germany) and weighed to calculate SLA values.

At the end of the growing season, after the end of insect collecting, the plants were cut down (Jagodziński et al., 2012). We decided that the best solution for comparing insect numbers was to convert the plants into a unit of leaf mass, taking into account their real, final mass. We realise that during the growing season, the mass of leaves changed with their growth, loss caused by folivorous insects and the production of new leaves as a defence mechanism of plants.

From each plant, all the leaves were collected to determine their fresh mass. The dry mass of the leaves of each plant was calculated based on a fresh–dry mass conversion factor, obtained by weighing a fresh leaf sample (200 g/plant), drying it at 65 °C and then re-weighing it.

## Methods of arthropod collection

Collection of arthropods was carried out throughout the growing season, from the onset of the first leaves on the plants (beginning of April) until the beginning of their descent (October). Collection was

carried out at two-week intervals, alternating during the day and at night, to obtain the most complete spectrum of insect species associated with the examined plants. Collecting was carried out between 11:00 and 13:00 during the day, and between 23:00 and 1:00 during the night.

The taxonomic affiliation of the collected insects and their number on individual plants was determined. The dynamics of abundance of individual species was not studied, only the total number at the end of the season, which was used only for relative estimates. This allowed us to assess the impact of plant species, light conditions and interactions between the two on arthropod fauna. Arthropod species were assigned to trophic groups based on literature data.

Collection mainly involved shaking the plants. Under the selected plants, a plastic foil was laid with an area not smaller than the area of the projection of the crown. The foil was square in shape and was cut from one side to the centre, so that the trunk of the plant was in the centre. After unfolding of the foil, the entire plant (shrub) was shaken intensively and the trunk (or trunks) was hit with a pole secured with felt. Following this shaking, any small organisms that fell on the foil were collected immediately using tweezers or an exhaustor.

The collected material was packed into plastic containers and segregated immediately. Unidentified larvae (e.g. caterpillars) were placed in boxes and kept until they transformed into imago, which enabled their subsequent identification. Arachnids were euthanised and preserved in 70% alcohol. The remaining organisms were killed with ethyl acetate, dry-formed, identified and catalogued. For the purpose of this study, analysis of results excluded Homoptera (including aphids, Aphidae) and Heteroptera, because they do not cause leaf damage in the form of biting. All bugs that are potential predators for folivorous insects, however, were included.

To fully identify species found on plants, we used sticky bands. These were put in place at the beginning of the growing season, before insects (especially larvae) awakened from winter diapause. At a height of approximately 30 cm above the ground, each plant's trunk was wrapped with 15 cm-wide polyurethane tape. If the shrub had several trunks, a separate strip of tape was placed around each trunk. The tape was lubricated with a special glue (sticky compound for insect traps; The Tanglefoot Company, Grand Rapids MI 49504-6485, USA) that is resistant to drying out and weather conditions. After two weeks, the tape strips were removed and the insects adhered to them were carefully peeled off with hexane, dissected and identified.

Summarised data regarding insect occurrence over the whole growing season were used to determine

Table 1. Light conditions of leaf growth, characterised by the specific leaf area (SLA), for plant species ( $n = 3$ ) growing under high light (HL) and low light (LL) conditions. The standard error (SE) values are given in brackets

Species	SLA [ $\text{cm}^2 \text{g}^{-1}$ ] ( $\pm$ SE)		
	HL	LL	
<i>C. sanguinea</i>	232.2 (23.7)	274.8 (21.3)	
<i>S. nigra</i>	165.0 (8.4)	303.4 (21.4)	
<i>F. alnus</i>	228.2 (3.2)	326.1 (12.1)	
<i>P. serotina</i>	170.2 (8.1)	206.9 (11.8)	
<i>P. padus</i>	153.0 (4.9)	164.1 (9.0)	
<i>C. avellana</i>	270.6 (8.4)	304.9 (8.3)	
ANOVA	df	F	P
Species (S)	5	33.2864	<0.0001
Light (L)	1	70.1338	<0.0001
S $\times$ L	5	7.4008	0.0003
error	24		

the density of insects, i.e. the number of specimens of a particular species (or at least genus) per kilogram of dry leaf matter. These data were the total numbers of insects collected by us on all dates, converted into a unit of dry mass of all leaves, determined after the last harvesting of insects (in autumn). The order, family and genus (or another higher taxonomic unit, as in the case of arachnids and robber flies) to which each species belongs are presented in table. In the case of insects, if species identification was impossible, only the generic name was given. The valid species names are according to the nomenclature of the Fauna Europaea Web Service (ver. 2019.10; fauna-eu.org). These data were therefore used only for relative comparisons, namely comparing numbers of insects among particular species (taxa), as well as among species of plants and light conditions. In addition, using these data and the SLA values calculated for each species of shrub under two light conditions (Table 1), it is simple to calculate, if necessary, the number of insects of a given species ( $n$ ) based on per unit dry mass of the leaves ( $n \text{ kg}^{-1}$ ), per unit of the surface or total projection (upper and lower) of the leaf surface ( $n \text{ m}^{-2}$ ).

## Data analyses

All analyses were conducted using the statistical analysis software JMP 8.0 (SAS Institute, Cary, NC, USA). A two-way ANOVA model was used to compare the specific leaf area (SLA) of six plants species growing in two different light conditions. To compare the numbers of insects found on shrubs, average values of insect species for the each treatment were calculated, on the basis of this percentage share of insect occurrence of a given species in the pool of all species. To determine the dominant species of herbivores and zoophages found on shrubs,

the dominance coefficient  $D = 100 \times (S_a / S)$  was used, where  $S_a$  is the sum of specimens belonging to species  $a$  in all tested samples and  $S$  is the sum of specimens of the test group of species in all samples (Trojan, 1978). The dominant species of insects in a given treatment were those for which the value of  $D$  was at least 5%, which is a well-known limit in ecology (Trojan, 1978).

To establish similarities in the occurrence of insect species between treatments (i.e. species of shrubs growing under specific lighting conditions), the Sørensen similarity coefficient  $S_o = 100 \times 2c / (a + b)$  was used, where  $c$  is the number of insect species common to two treatments,  $a$  is the number of species in the first treatment and  $b$  is the number of species in the second treatment (Whittaker, 1972; Trojan, 1978). These data are presented in order of plant species from least to the most damaged by folivores, further divided based on the light conditions in which they grew. Only *C. avellana* was placed at the end of the diagram, due to the very different relationships is exhibited between the degree of leaf damage and light conditions.

## Results

Based on our systematically conducted collection, we have compiled a list of insect, arachnid and myriapod species, as well as density data of arthropods found on six plant species, under differing light conditions (Table 2). In total, on six understory plant species and under both light conditions, we found 153 taxa of arthropods, including a few only unidentified to the level of taxonomic groups such as spiders (Araneae), harvesters (Opiliones), sand wasps (Sphecidae) and robber flies (Asilidae), or individual genus, such as *Lithobius* or *Melighetes* (Table 3). Within the entire collection, we distinguished 43 species of folivores, 27 species of other herbivores, 52 species of zoophages, and 44 species belonging to other trophic groups. The greatest species richness was found on *P. serotina*, *P. padus* and *C. sanguinea* (72 – 73 species) and the smallest variety was on *F. alnus* (44 species).

## Influence of plant species on the occurrence of herbivorous insects

The most common insect appearing on the studied plant species (Fig. 1), was *Gonioctena quinquepunctata* Fabricius, a beetle from the family Chrysomelidae (over 40% of the total number of individuals, i.e. on all plant species). The greatest number of *G. quinquepunctata* was found on *P. padus* (14.4%) and *P. serotina* (12%). This beetle was also the only folivorous

Table 2. Numbers of herbivorous and predatory arthropods collected from plants growing in high light (HL) and low light (LL) conditions, per kilogram of dry mass of leaves (+ indicates that a single individual was found)

Order / Family / Genus / Species	<i>C. sanguinea</i>		<i>S. nigra</i>		<i>F. alnus</i>		<i>P. serotina</i>		<i>P. padus</i>		<i>C. avellana</i>		
	HL	LL	HL	LL	HL	LL	HL	LL	HL	LL	HL	LL	
<b>CHELICERATA</b>													
Arachnida													
Araneae	55.0	76.7	77.2	112.2	135.4	422.8	62.4	32.6	58.6	90	33.8	33.4	
Opiliones		1.4	6.9	7.5	6		1.4	2.3	1.7		0.7	0.9	
<b>MYRIAPODA</b>													
Lithobiidae													
<i>Lithobius sp.</i> Leach	+	+	5.2	4.8	13.2	19.3	8.5	1.7	5.1	2	2.9	1	
<b>INSECTS</b>													
<b>BLATTODEA</b>													
Blattellidae													
<i>Ectobius lapponicus</i> Linnaeus										+			
<i>Ectobius sp.</i> Stephens				+							+	+	
<b>COLEOPTERA</b>													
Anthicidae													
<i>Notoxus monoceros</i> Linnaeus	+		+	+			+		+	+	+		
Anthribidae													
<i>Anthribus nebulosus</i> Forster							+	+					
<i>Enedreytes sepicola</i> Fabricius				1.6									
<i>Platystomos albinus</i> Linnaeus												+	
Apionidae													
<i>Protapion fulvipes</i> Geoffroy												0.7	
<i>Oxystoma cracca</i> Linnaeus				1.6		19.3	1.4	0.3				0.7	0.6
Attelobidae													
<i>Apoderus coryli</i> Linnaeus	+												+
Byturidae													
<i>Byturus ochraceus</i> Scriba										4.7			
Cantharidae													
<i>Cantharis livida</i> Linnaeus			+										
<i>Cantharis nigricans</i> Muller	4.5	6.6		+	6		+	0.6	2.5	+		0.5	
<i>Cantharis obscura</i> Linnaeus							+						
<i>Cantharis pellucida</i> Fabricius			+	2.4									
<i>Cantharis rustica</i> Fallen			1.4										
<i>Rhagonycha fulva</i> Scopoli			3.1										
<i>Rhagonycha lignosa</i> Muller	1.5			+	7.3			1		2	1.1	1	
<i>Malthinus sp.</i> Latreille					6.0								
Carabidae													
<i>Amara aulica</i> Panzer			4.5	1.6							+		
<i>Demetrias atricapillus</i> Linne			9.4	5.7			1.1			+	+	0.6	
<i>Limodromus assimilis</i> Paykull			8.3	2									
Cerambycidae													
<i>Alosterna tabacicolor</i> De Geer					19.9	+	1.6				2.5		
<i>Anaglyptus mysticus</i> Linnaeus								0.8	1.7				
<i>Clytus arietis</i> Linnaeus									+				
<i>Cortodera femorata</i> Fabricius				+				+	+				
<i>Cortodera humeralis</i> Schaller										+			
<i>Dinoptera collaris</i> Linnaeus		6.6			7.3								
<i>Grammoptera ruficornis</i> Fabricius	+		1.4	2.4	6.0	19.3	1.9	0.3					
<i>Leiopus nebulosus</i> Linnaeus								+					
<i>Menesia bipunctata</i> Zoubkoff					+								
<i>Molorchus minor</i> Linnaeus							+	+					
<i>Oberea linearis</i> Linnaeus											+		
<i>Obrium brunneum</i> Fabricius							+	+					
<i>Pogonocherus hispidus</i> Linnaeus	0.8	2.7	+	2.4		+		+		2	0.7		
<i>Rhagium mordax</i> De Geer							+		2.5				



Order / Family / Genus / Species	<i>C. sanguinea</i>		<i>S. nigra</i>		<i>F. alnus</i>		<i>P. serotina</i>		<i>P. padus</i>		<i>C. avellana</i>	
	HL	LL	HL	LL	HL	LL	HL	LL	HL	LL	HL	LL
<i>Cidnopus aeruginosus</i> Olivier			6.6		16.6	+						
<i>Dalopius marginatus</i> Linnaeus	4.3	5.5		9.5	6.6	45	19.3	9.2	19.9	17.2	6.7	1.2
<i>Denticollis linearis</i> Linnaeus				2.9								+
<i>Dicronychus cinereus</i> Herbst		2.7	+	+		27.3	2.8	1.5	4.3	3.7	1.6	1
<i>Ectinus aterrimus</i> Linnaeus						+	1.7	0.6	1.7	2		+
<i>Hemicrepidius niger</i> Linnaeus			1.4	2.4								
<i>Melanotus villosus</i> Fourcroy											0.6	+
<i>Prosternon tessellatum</i> Linnaeus											0.5	+
Latridiidae												
<i>Corticicara gibbosa</i> Herbst	+	+	+	+				+	+	+	+	
Malachiidae												
<i>Malachius bipustulatus</i> Linnaeus				1.6								
Melandryidae												
<i>Osphyra bipunctata</i> Fabricius							+	+				
Nitidulidae												
<i>Epuraea</i> sp. Erichson					6							
<i>Meligethes</i> sp. Stephens	+	+	+	+	+		+	+	+	+		+
Phalacridae												
<i>Olibrus bimaculatus</i> Kuster				+								
<i>Phalacrus corruscus</i> Panzer						+					+	+
<i>Stilbus testaceus</i> Panzer			+	+							+	
Ptinidae												
<i>Ernobius longicornis</i> Sturm								+				
<i>Ptinomorphus imperialis</i> Linnaeus				+						+		
<i>Ptinus rufipes</i> Olivier								+				+
Pyrochroidae												
<i>Schizotus pectimicornis</i> Linnaeus												+
Rhynchitidae												
<i>Byctiscus betulae</i> Linnaeus	+										+	+
<i>Neocoenorrhinus pauxillus</i> Germar							1.1	1.5		2		
Scarabaeidae												
<i>Cetonia aurata</i> Linnaeus			+	+								
<i>Melolontha melolontha</i> Linnaeus		+	+		+					+		
<i>Phyllopertha horticola</i> Linnaeus			+					0.8	+		+	
<i>Serica brunnea</i> Linnaeus		2.7	3.8			33.7				2.1		
Scaptiidae												
<i>Anaspis frontalis</i> Linnaeus	4.3	13.1	5.6	4.7	46.4	90.6	68.3	49.4	5.2	9.8		
Silphidae												
<i>Dendroxena quadrimaculata</i> Scopoli							+					
Staphylinidae												
<i>Paederus fuscipes</i> Curtis			24.4									
<i>Stenus humilis</i> Erichson								1.4				
<i>Tachinus lignorum</i> Linnaeus			1.4	21								
<i>Tachyporus hypnorum</i> Fabricius	1.1	15.2	10.4						1	5.1		
<i>Tachyporus solutus</i> Erichson	3.5					27.3				3.1	4.5	1.7
Tenebrionidae												
<i>Diaperis boleti</i> Linnaeus												+
<i>Gonodera luperus</i> Herbst	+	+										+
<i>Lagria hirta</i> Linnaeus		+	5.2	2.7			1.1	1.5	2.1	2.3		
Throscidae												
<i>Trixagus carinifrons</i> Bonvouloir							+					
<i>Trixagus dermestoides</i> Linnaeus	+											
DERMAPTERA												
Forficulidae												
<i>Chelidura acanthopygia</i> Gene			+	4.7		82		+	7.3	+	1.4	
<i>Forficula auricularia</i> Linnaeus	1.7	3.4	13.0	6.8	+	+	1.5	2	+	14.6	+	1.4



Order / Family / Genus / Species	<i>C. sanguinea</i>		<i>S. nigra</i>		<i>F. alnus</i>		<i>P. serotina</i>		<i>P. padus</i>		<i>C. avellana</i>	
	HL	LL	HL	LL	HL	LL	HL	LL	HL	LL	HL	LL
DIPTERA												
Asilidae	0.8								4.7		+	0.9
HETEROPTERA												
Thyreocoridae							3.4	0.8				0.5
<i>Thyreocoris scarabaeoides</i> Linnaeus			+									
Nabidae												
<i>Himacerus apterus</i> Fabricius		+	+	+	+			+	+			
<i>Himacerus mirmicoides</i> O. Costa	+								+		+	
Reduviidae												
<i>Rhynocoris iracundus</i> Poda												+
HYMENOPTERA												
Diprionidae												
<i>Gilpinia sp.</i> Benson							1.1					
Formicidae												
<i>Formica polyctena</i> Forster		+					+					
<i>Formica sp.</i>	+								+	+		
Sphecidae							+					
LEPIDOPTERA												
Erebidae												
<i>Callimorpha dominula</i> Linnaeus		+							+			
<i>Calliteara pudibunda</i> Linnaeus									+			0.5
<i>Orgyia antiqua</i> Linnaeus	1.5	6.6			7.3		0.8	1	2.6	2.1		
<i>Euproctis chrysorrhoea</i> Linnaeus							1.6			3.2		0.9
<i>Euproctis similis</i> Fuessly	2.1	6.6						2		2.0	0.7	
Lasiocampidae												
<i>Malacosoma neustria</i> Linnaeus								+	+			
Noctuidae												
<i>Mythimna albipuncta</i> Denis & Schiffmüller				2.4								
Yponomeutidae												
<i>Yponomeuta evonymella</i> Linnaeus									1.7	3.2		
NEUROPTERA												
Chrysopidae												
<i>Chrysoperla carnea</i> Stephens			+					+				
<i>Chrysopa sp.</i> Steinmann		+			+				+		+	+
ORTHOPTERA												
Meconematidae												
<i>Meconema thalassinum</i> De Geer	1.5	1.4		+	+		0.8	3.1	1		1.1	2.9

Table 3. Species of arthropods identified on six species of understory shrubs, divided into trophic groups

Trophic group	<i>C. sanguinea</i>	<i>S. nigra</i>	<i>F. alnus</i>	<i>P. serotina</i>	<i>P. padus</i>	<i>C. avellana</i>
Predator	24	26	16	25	23	23
Predator/Herbivore	3	2	2	2	1	3
Predator/Palynivore	0	1	0	0	0	0
Herbivore	11	12	10	12	14	11
Folivore	17	13	11	18	23	18
Xylophage	0	1	0	3	0	1
Palynivore	1	1	1	1	2	1
Mycophage	0	0	0	1	0	1
Polyphage	1	1	1	1	1	1
Saprophage	4	9	1	8	5	8
Undetermined	1	6	2	2	3	2
Total number of species	62	72	44	73	72	69

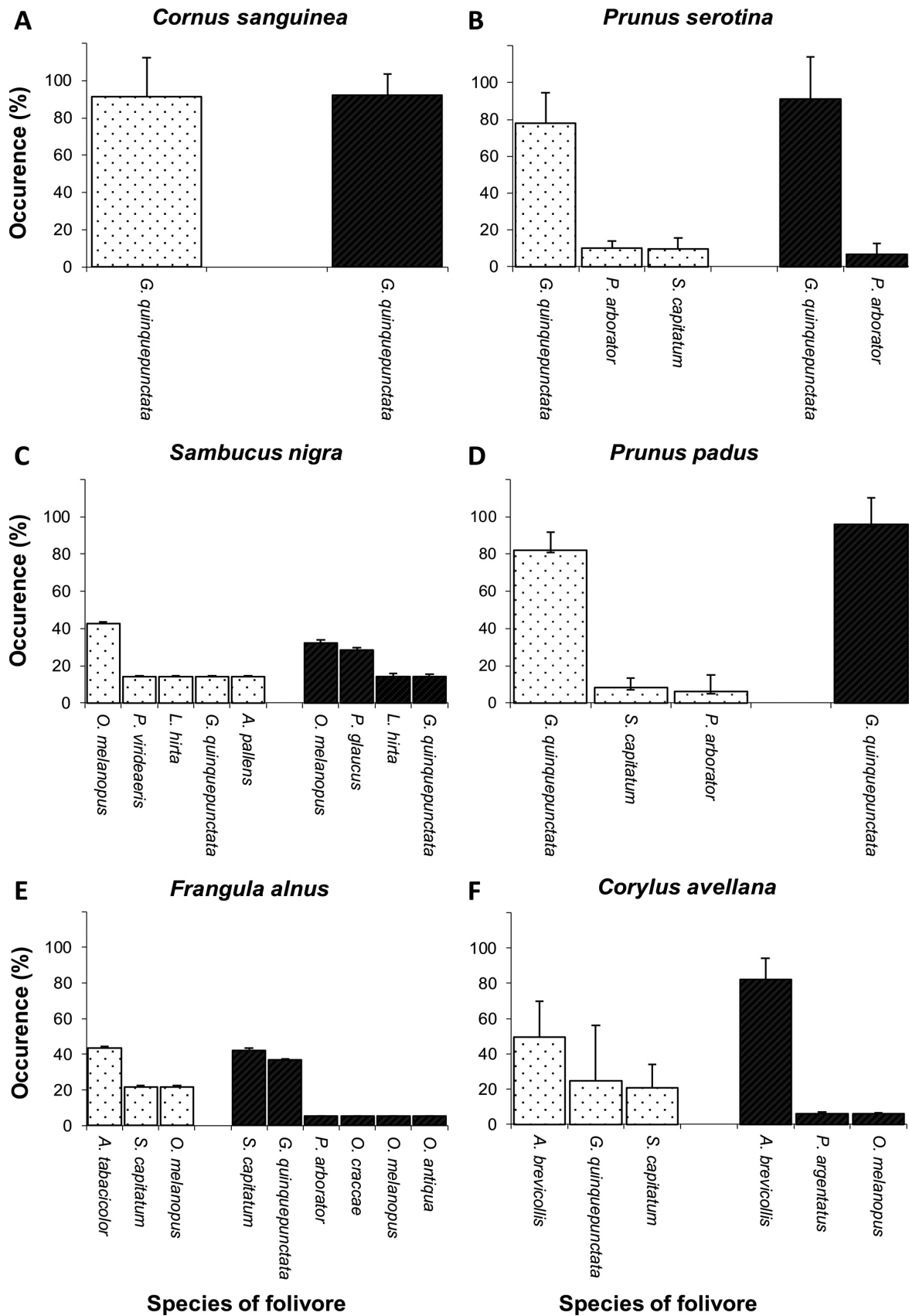


Fig. 1. Species of dominating folivores (comprising 5% or more of the total number of folivores on the plant) on six plant species growing under two light conditions. White columns – low light conditions (LL), black columns – high light conditions (HL). Thin bars indicate standard error. Vertical segments on graphs mark the values of standard error (SE) of the means for three plants, treated as a sum

species found on *C. sanguinea* (Fig. 1A). On *S. nigra* the leaf beetle *Oulema melanopus* Linnaeus (Coleoptera: Chrysomelidae) was dominant (Fig. 1C). On *C. avellana*, the most frequently encountered folivore was another beetle from the Chrysomelidae family, *Altica brevicollis coryletorum* Král (9% of the total population of folivores on *C. avellana*; Fig. 1F). On *F. alnus*, the dominant folivores were *Alosterna tabacicolor* (De Geer) and *Strophosoma capitatum* (De Geer) (Fig. 1E).

When species diversity of folivores was analysed in relation to the leaf damage they caused, a relatively large number of dominant species of folivores were found on species showing weak (*S. nigra*) and moderate (*F. alnus*) damage (Fig. 1C, E). Conversely, for another species that also showed weak leaf damage (*C. sanguinea*), the dominant folivore was exclusively a polyphagous beetle, *G. quinquepunctata* (Fig. 1A). This same beetle accounted for over 90% of all folivores feeding on plant species exhibiting weak damage. This folivore was also found in a large number (>80% of all individuals of the insect species dominant on the plant species) on both strongly injured plant species in the genus *Prunus* (Fig. 1B, D). In contrast to the weakly injured *C. sanguinea* (Fig. 1A), however, species other than *G. quinquepunctata* exceeded 5% of the total number of insects on *Prunus* species (Fig. 1B, D).

Based on the Sørensen coefficient, similarity in the occurrence of folivorous species (Fig. 2) on

the examined plants was greater within plant species (between light conditions) than among plant species. The most similar composition of folivores was found between *P. padus* and *P. serotina* (59.1%, on average in both light conditions), followed by the similarity between *F. alnus* and *C. sanguinea* (52.3%), and between *F. alnus* and *P. serotina* (50.1%; Fig. 2). *Corylus avellana* hosted the fewest common species of folivores, even fewer than those on *C. sanguinea* (29.9%) and *P. padus* (33.3%). Relatively few common species of folivores were found on leaves belonging to the least damaged species, *S. nigra* and *C. sanguinea* (35.4%).

An analysis similar to that conducted for folivores was carried out for herbivorous species in general (Fig. 3). In the examined shrub species, the presence of herbivores (45.3%) was very similar to that of folivores (43.3%; averaged under both light conditions together). The similarity in herbivorous species on *F. alnus* and *P. serotina* (71.0%) was even higher than in the case of only folivores, but was slightly smaller between the two species of *Prunus* (52.8%). In contrast, for plant species characterised by low similarity in folivores, the species composition of herbivores showed much greater similarities (39.1% between *C. avellana* and *C. sanguinea*, and 51.3% between *S. nigra* and *C. sanguinea*). The lowest similarity in herbivores was between *C. avellana* and *S. nigra* (14.6%), and was 3.4 times smaller than that for folivores (48.9%).

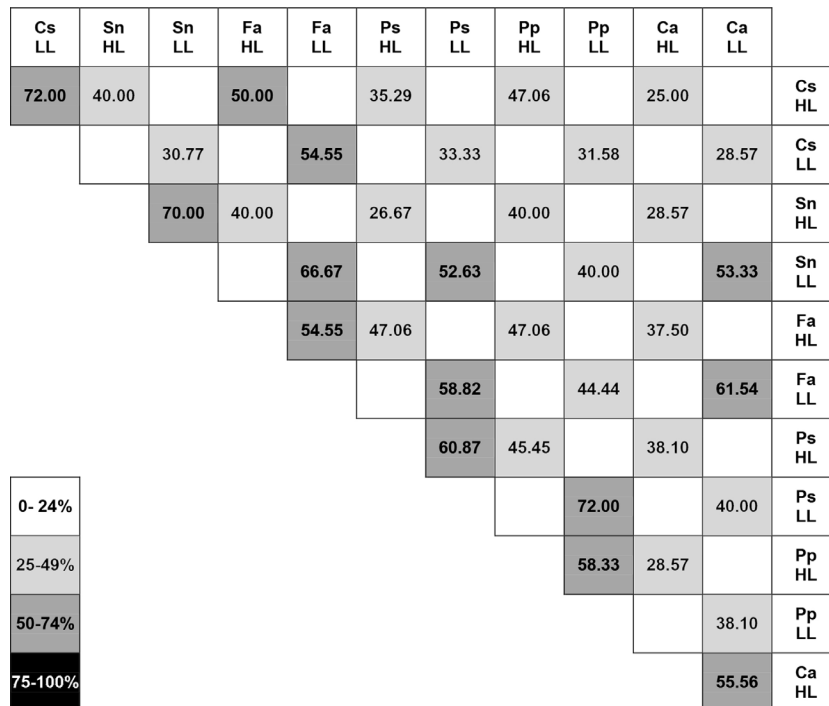


Fig. 2. Sørensen similarity coefficients of folivores on six plant species in two light conditions. A darker field indicates that the degree of similarity is higher. Symbols denote the six studied plant species: Cs – *Cornus sanguinea*, Sn – *Sambucus nigra*, Fa – *Frangula alnus*, Ps – *Prunus serotina*, Pp – *Prunus padus* and Ca – *Corylus avellana*. HL – high light, LL – low light

## Influence of light conditions on the occurrence of herbivorous insects

In most plant species, light influences the number of dominant insect species that feed on the plant (Fig. 1). Thus, this study obtained a much wider species spectrum of dominant folivores on *S. nigra*, *F. alnus* and both species of *Prunus* than would typically be observed for high or low light conditions separately. The species of folivores most commonly represented under both light conditions (HL and LL) also proved to be dominant under each light condition separately. In the case of both *Prunus* species with strongly damaged leaves, *G. quinquepunctata* was the most abundant folivore under both light conditions (Fig. 1B, D). When growing in HL only, however, both *Prunus* species hosted folivores of two other dominant species – *S. capitatum* and *Phyllobius arborator* (Herbst) from Curculionidae. On *C. sanguinea* with weakly damaged leaves, *G. quinquepunctata* was also dominant and, in fact, only species dominating in both light conditions together and separately (Fig. 1A). A similar relationship occurred with *A. brevicollis coryletorum* feeding on *C. avellana* (Fig. 1F) and with *O. melanopus* found on *S. nigra* (Fig. 1C). On *C. avellana*, however, *G. quinquepunctata* was much more common (over 80%) on shrubs that were sunlit than on those in the shade (50%).

When assessing all examined species of plants, the average value of the similarity of occurrence of folivorous species between the two light conditions

was 61.7%. This value is higher than the similarity in folivores between plant species (HL and LL together), which amounted to 43.3%. When comparing the number of folivorous species between HL and LL treatments (Fig. 2), we observed the greatest similarity between light conditions in plant species weakly damaged by herbivorous insects, such as *C. sanguinea* (72%) and *S. nigra* (70%). For other species of shrubs this similarity was smaller, ranging from 54.5% in *F. alnus* to 60% in *P. serotina*.

The similarity in herbivorous species between LL and HL conditions (on average in all plant species) was 61.9% (Fig. 3), very similar to that of folivores (61.7%). Interestingly, a high similarity of occurrence of herbivorous species was found for *C. sanguinea* (85.7%), but not *S. nigra*, despite the fact that both plant species were weakly damaged by insect feeding. Indeed, the similarity in herbivores between light conditions was extremely low for *S. nigra*, on par with strongly damaged *P. padus* (near 40% for both). The highest similarity between light conditions was observed for *P. serotina* (88.9%), which was moderately damaged by insect feeding.

## Zoophages on various species of plants

The dominant zoophagous invertebrates are arachnids. In the current study, arachnids were not determined to the species level. All calculations of the number of arachnids present concerned their two large systematic groups – the proper spiders

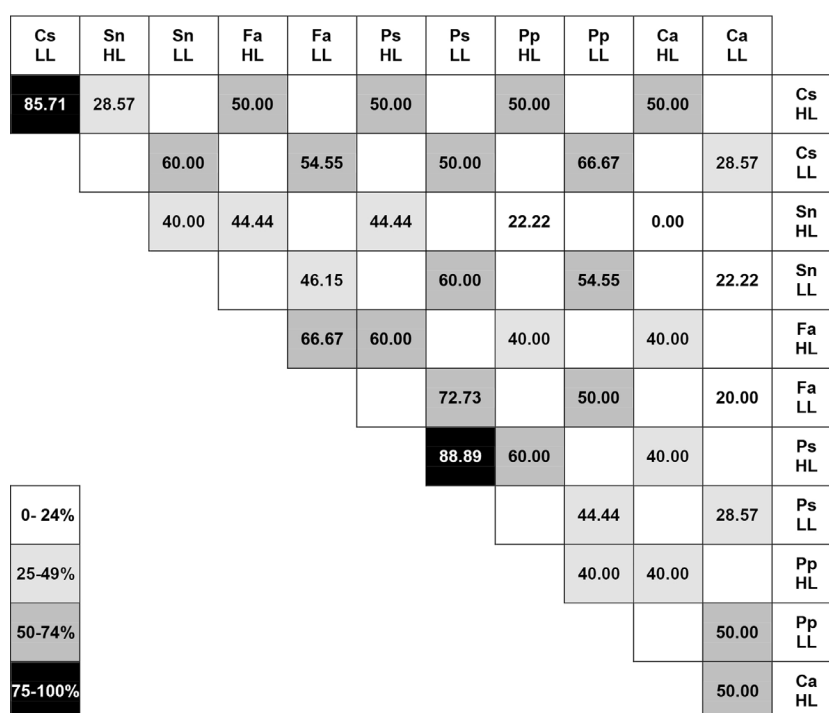


Fig. 3. Sørensen similarity coefficients of herbivores on six plant species in two light conditions. A darker field indicates that the degree of similarity is higher. See Fig. 2 for explanation of symbols

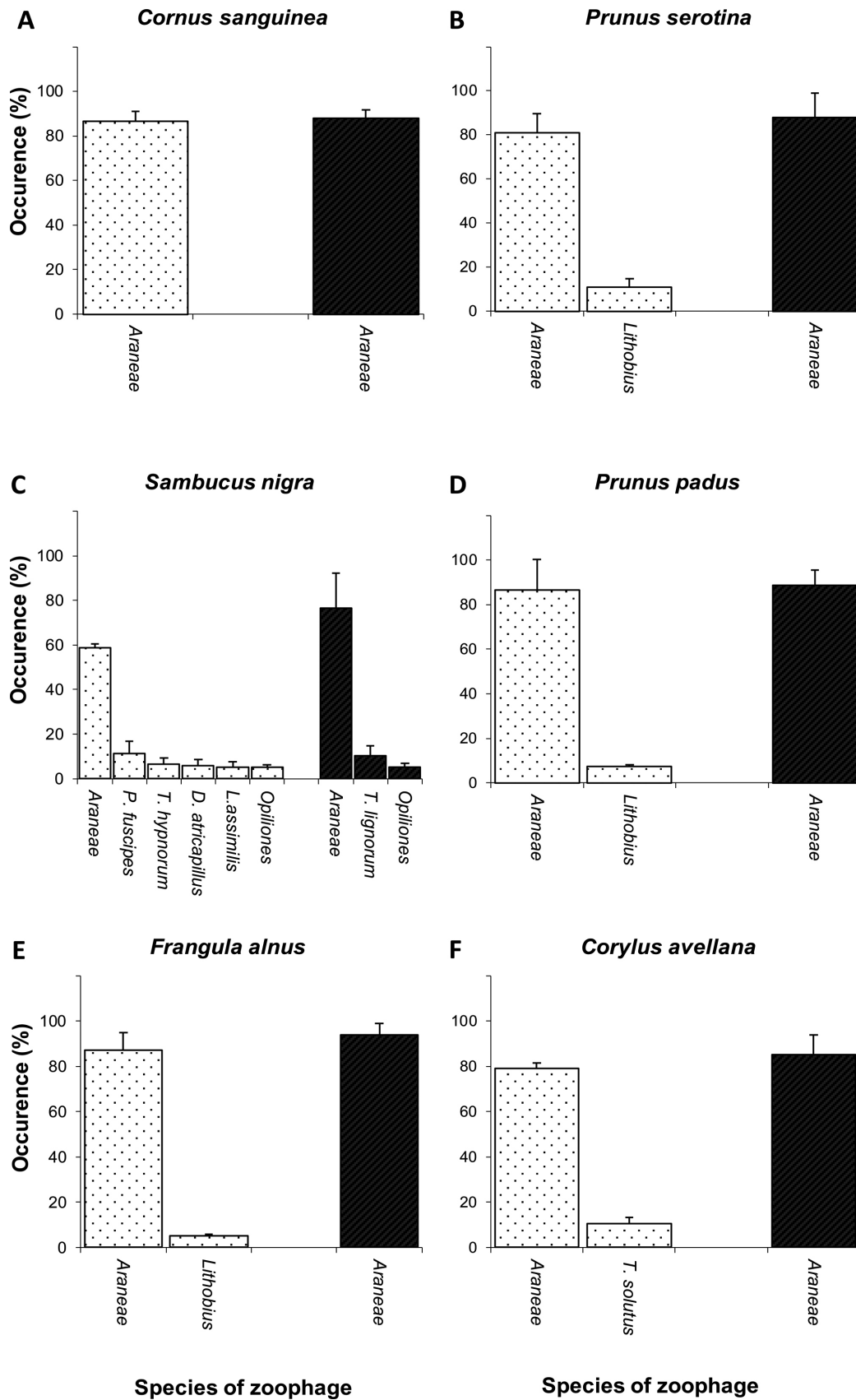


Fig. 4. Species of dominating zoophages (comprising 5% or more of the total number of zoophages on the plant) on six plant species growing under two light conditions. White columns – low light conditions (LL), black columns – high light conditions (HL). Vertical segments on graphs mark the values of standard error (SE) of the means for three plants, treated as a sum

(Araneae) and harvesters (Opiliones). On all species of plant, the most common group of predators was spiders (Araneae, Fig. 4). On both *S. nigra* and *C. avellana*, there was a clear dominance of beetles from the Staphylinidae family, with *Tachyporus lignorum* Linnaeus on *S. nigra* and *T. solutus* (Erichson) on *C. avellana*. Both *Tachyporus* species constituted over 6% of the predatory fauna hunting on the examined plant species. On *S. nigra*, there were also many members of Opiliones, and on *P. serotina*, centipedes belonging to a species of *Lithobius* (Leach) made up nearly 8% of the population of predators present. The diversity of dominant predatory species on *S. nigra*, as with the abundance of folivores, likely resulted from the small abundance of zoophagous species.

Comparing Sørensen coefficients among individual species (HL and LL together) showed a relatively large diversity of zoophages present on different plant species (Fig. 5). The lowest similarity in zoophagous species (taxa) occurred between plants weakly damaged by folivores, i.e. *S. nigra* and *C. sanguinea* (27%). Similarities in zoophagous species were more than twice as great among species of plants with different levels of damage by folivores, with a similarity of 66% between *F. alnus* and *C. avellana*, 65.2% between *C. sanguinea* and *C. avellana*, and 63.1% between *P. serotina* and *C. avellana*.

## Influence of light conditions on the occurrence of zoophages

The dominant group of predatory species collected from plants was spiders (Araneae), and the second group consisted of predators from the genus *Lithobius*. There were no large differences in the diversity of predators between light treatments in most plant species (Fig. 4). Four plant species (*P. serotina*, *P. padus*, *F. alnus* and *C. avellana*; Fig. 4B, D – F) exhibited two dominant taxa of zoophages in HL, but only one in LL. In HL, there were not large numbers of predators belonging to the two taxa and none of them exceeded 10%. On *S. nigra*, however, there were three taxa present in LL conditions, and three more taxa of dominating zoophages in HL, but also with small numbers (<10%).

Similarities in zoophage occurrence between the two light treatments varied among the examined species (Fig. 5; 46.2 – 77.8%). In this analysis, the spiders (Araneae) and harvesters (Opiliones) were considered together. The greatest similarity in zoophagous species between HL and LL was found on *C. avellana* (77.8%). This is the opposite of results for herbivorous insects, where *C. avellana* exhibited a much lower similarity between HL and LL than did other plant species, with 55.6% similarity for folivores and 50% for herbivores.

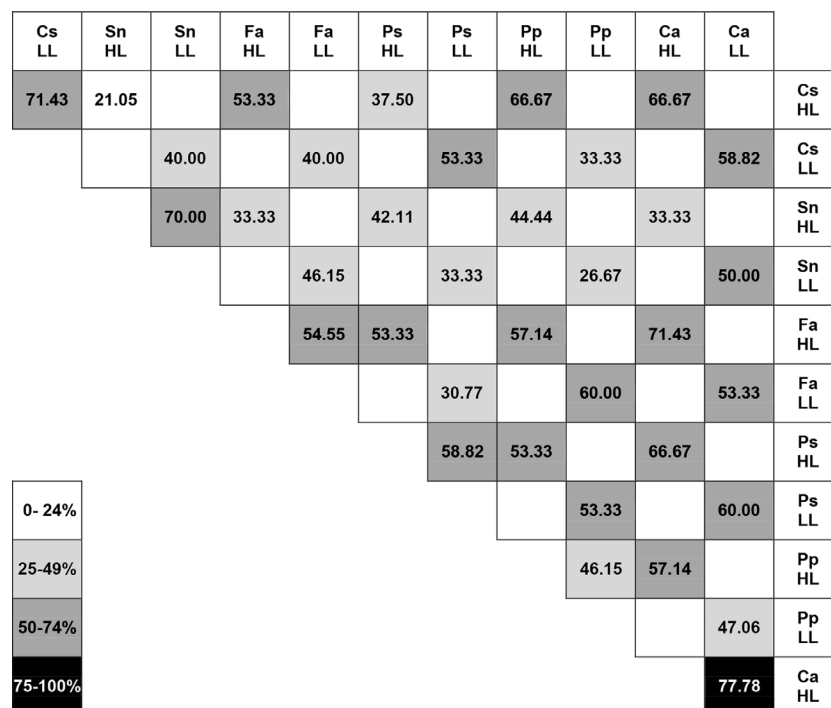


Fig. 5. Sørensen similarity coefficients of zoophages on six plant species in two light conditions. A darker field indicates that the degree of similarity is higher. See Fig. 2 for explanation of symbols

Relatively high similarities in zoophagous species between HL and LL were also found for the plants most resistant to folivore feeding – *C. sanguinea* (71.4% similarity) and *S. nigra* (70%). *Prunus serotina* exhibited an average 58.8% similarity in zoophagous species between HL and LL, whereas on *P. padus* the similarity was the lowest (46.2%). The similarity in zoophagous species between HL and LL for a plant moderately damaged by folivores, *F. alnus*, was slightly lower (54.6%) than that of *P. serotina*. In addition, a comparison of Sørensen coefficients (Fig. 5) showed that the similarity of occurrence of zoophagous species between the examined plants was slightly higher in HL conditions (50.5%) than in LL (45.7%), which is the opposite of that for folivorous and herbivorous species.

### Folivores vs. zoophages

The number of zoophagous species present on the six species of plants we examined ranged from 16 to 26 (Table 3), whereas the number of herbivorous species present ranged from 21 on *F. alnus* to 37 on *P. padus*. The ratio of the number of folivorous to zoophagous species varied among plant species,

but there were always more herbivorous species. Herbivores had the greatest advantage over predators in the most damaged plant species (*P. padus*; ratio 1.6), whereas weakly damaged species such as *C. sanguinea* and *S. nigra* exhibited ratios of 1.2 and 1.0, respectively.

These relationships are more complete and transparent when we analyse them separately for each light condition (HL, Fig. 6A; LL, Fig. 6B), and separately for folivores and zoophages. Such analysis showed that only *P. padus* and *C. avellana* have a clear dominance of folivorous species over predators under any light conditions. On *P. serotina*, *C. sanguinea* and *F. alnus*, however, the same dominance only takes place in the case of plants growing in LL, whereas in HL the numbers of folivorous and zoophagous species are very similar. Out of all the plant species studied here, it was clear that on *S. nigra*, regardless of light condition, the number of predatory species was greater than the number of folivorous species (ratio of 2.1 in HL and 1.3 in LL).

For some plant species, the number of specimens and the ratio of folivores to zoophages is more important than species diversity when we are looking for causes of different degrees of leaf damage. We

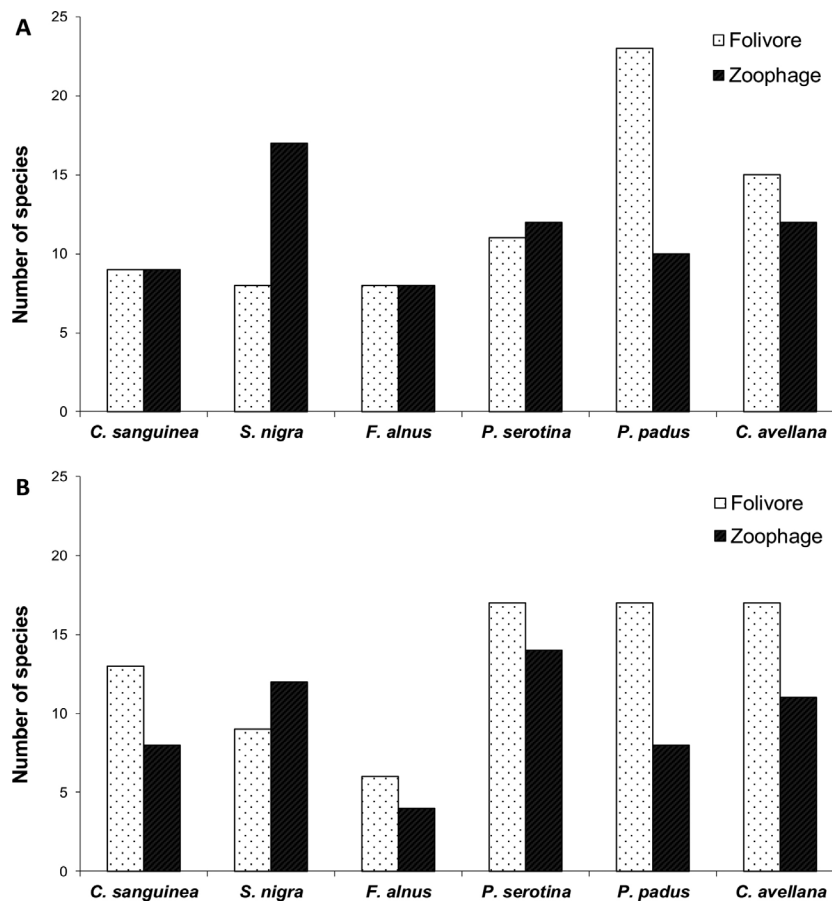


Fig. 6. The total number of species of folivores (white columns) and zoophages (black columns) occurring on six plant species growing in high light (A) and low light (B) conditions

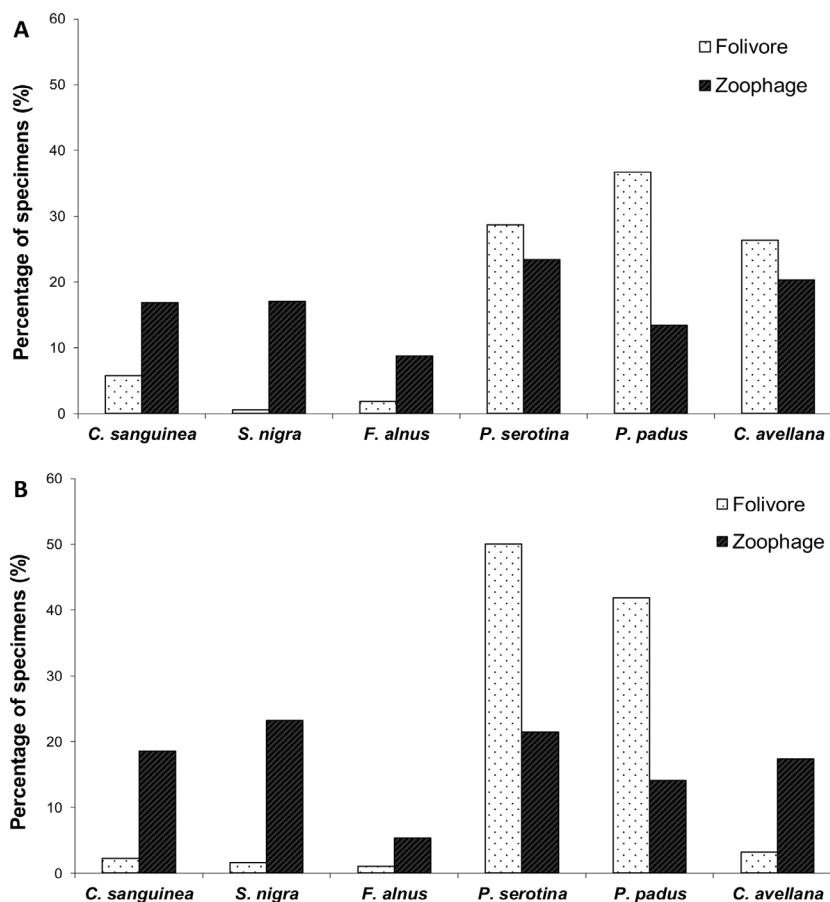


Fig. 7. The percentage of the total number of specimens represented by folivores (white columns) and zoophages (black columns) occurring on six plant species growing in high light (A) and low light (B) conditions. The sum of all folivores or zoophages occurring on all plants of a given light treatment was 100%

found that for plants with weak (*C. sanguinea* and *S. nigra*) and moderate (*F. alnus*) levels of leaf damage, the number of zoophages was several times (occasionally more than ten) greater than the number of folivores (Fig. 7). This relationship was observed under both light conditions. In plants with more damaged leaves (*P. padus* and *P. serotina*), the reverse appeared to be true, with the total number of folivores being greater than the number of zoophages. In *P. padus*, these relationships were similar under both light conditions. In *P. serotina* the dominance of folivores over zoophages in HL was not as large as in LL. For *C. avellana*, light conditions had a different effect on the ratio of folivore and zoophage abundance – folivores outnumbered predators only in HL, whereas in LL, due to the small number of folivores, the number of zoophages exceeded folivores by 5.1 times.

## Discussion

We believe that the results of our research will contribute to broadening the body of knowledge regarding entomofauna on the most commonly

occurring understory plants in Central and Eastern Europe. We have not limited our study to folivores, but have also included general herbivores, as well as predatory insects and arachnids (zoophages) that prey upon them. This work also shows the important ecological role predators play in maintaining stability in communities. The species diversity of these entomofauna differed not only among plant species but, in some cases, also depended on lighting conditions. The results of this study also allowed for relative comparisons of numbers among insect species and trophic groups (Table 2 and 3), for each species of plant and under two light conditions. Together, qualitative and quantitative data helped in understanding the differences among the examined plant species concerning the susceptibility of leaves to insect feeding, as well as highlighting differences related to light conditions. We are aware that differences in species composition and abundance of arthropod fauna may be affected by differences between the micro-habitats of the studied plants. As we noted, in Materials and Methods the habitat in which the plants grew was the same. The studied plants did not grow individually, but in groups of several plants of a given species.



## Influence of plant species on leaf damage by herbivores, herbivore diversity and herbivore abundance

When comparing the diversity of folivores and other herbivores with the degree of leaf damage caused by insects (percent of perforation due to feeding by insects), determined in earlier studies (Karolewski et al., 2013), we did not find simple and unambiguous relationships. Some trends, however, were observed. For example, both plant species weakly damaged (*C. sanguinea* and *S. nigra*) hosted relatively few common folivorous species. This may be because the leaves of these two species are very resistant to insect grazing. This is particularly evident in *C. sanguinea*, on which we found only one dominant polyphagous species, *G. quinquepunctata* (Fig. 1A). Evidently this insect species, known for its exceptionally wide and diverse food base (Mardulyn et al., 1997; Urban, 1998; Halarewicz & Jackowski, 2011) that can even include heavily polluted leaves (Łukowski et al., 2018), is also able to use *C. sanguinea*. In western Europe, this species is replaced by the similar species *G. pallida* L. (Leather, 1994; Mardulyn et al., 1997; Uusitalo, 2004). Duffey et al. (Duffey et al., 1974) also observed few herbivorous species feeding on *C. sanguinea*. Additionally, in controlled insect feeding studies, *C. sanguinea* leaves were found to be an inappropriate food for *Lymantria dispar* Linnaeus larvae (Heskova, 1973), although this insect also typically uses a very broad spectrum of broadleaved species (Sharov et al., 1999; Lazarević et al., 2002). In contrast, however, in the second plant species we studied that is typically resistant to herbivory, *S. nigra*, we found a relatively broad species diversity of dominant folivores (Fig. 1C). This does not correspond to the research of other authors, who have reported a relatively small number of folivorous species using *S. nigra* as food (Duffey et al., 1974; Atkinson & Atkinson, 2002). Our results indicate that plant species that suffer weak damage to leaves host few common species of folivores. The single common dominant species of folivore on both *C. sanguinea* and *S. nigra* was *G. quinquepunctata*. In addition, low abundance of folivorous species is typically associated with these plant species, likely due to the poor nutritional quality of their leaves (Karolewski et al., 2013). This low number of folivores was also confirmed by the results of Ward (Ward & Lakhani, 1977). Between these two plant species, we also found a low similarity of herbivorous species.

In contrast to species with leaves weakly injured by insects, strongly (*P. padus*) and moderately (*P. serotina*) damaged plants hosted a wider spectrum of folivores. The literature indicates that *P. padus* is associated with numerous species of folivorous and

herbivorous species (Leather, 1985, 1991; Uusitalo, 2004), as is *P. serotina*, despite being an alien species growing in Europe (Nowakowska & Halarewicz, 2006a, b; Halarewicz & Jackowski, 2011; Meijer et al., 2012). Both *Prunus* species host a relatively large percentage of common species of folivores and a slightly smaller percentage of herbivores. Great similarity of herbivorous species, mainly generalists, on the two *Prunus* species was also reported by Schilthuizen et al. (Schilthuizen et al., 2016), when conducting research in one of the National Parks in the Netherlands. These authors found a wider species diversity of herbivorous insects for *P. serotina* than for *P. padus*. We found the opposite, with 23 folivores and 14 other herbivores on *P. padus* (Table 3), and 18 folivorous and 12 herbivorous species on *P. serotina*.

It is generally assumed that the greater the distribution of a given plant species is, the greater the number of species of insects associated with it will be (Verberk, 2011). Leather (Leather, 1985) reported, however, that *P. padus* did not host a large variety of species of herbivorous insects, finding instead that out of 196 species of herbivores feeding on seven species in the genus *Prunus* in the UK, only 23 of those species were associated with *P. padus*. Not only folivorous insects include *P. serotina* in their food base; for example, seeds of *P. padus* and *P. serotina* grown in Belgium were damaged by an insect that typically feeds on seeds, the weevil *Furcicus rectirostris* Linnaeus (Vanhellemont et al., 2014). Based on a meta-analysis, Leimu and Koricheva (Leimu & Koricheva, 2006) suggested that if a plant is susceptible to feeding by generalist insects, it will be used by many species, not only one. One genus of folivore, however, has exhibited significant differences depending on whether it is using *P. padus* or *P. serotina* – the monophagous moth *Yponomeuta evonymella* Linnaeus. This species reluctantly uses new food plants (Leather & Lehti, 1982), and in recent years has been found using *P. serotina* as a host plant (Karolewski et al., 2014, 2017; Łukowski et al., 2017). Wider research concerning the use of foreign plant species by native insects was carried out in the Netherlands by Meijer et al. (Meijer et al., 2012), who found 99 species of native herbivores. This explains the high percentage of common species of folivores found on both *Prunus* species, as both species must cope effectively with the wide diversity and large number of insects through the production of new shoots, which takes place only after the end of the insect feeding period (Leather & Lehti, 1982; Uusitalo, 2004).

*Frangula alnus*, which leaves were moderately damaged, hosted a low diversity of folivores, even lower than the weakly damaged *C. sanguinea* and *S. nigra* (Table 3, Fig. 6A, B). The overall number of folivores on *F. alnus* was also small. Although *F. alnus* is a native species in Europe, no folivorous species

threatens it with more significant defoliation, with exception – *Orgyia Antiqua* Linnaeus (Gassmann et al., 2008). The lack of folivores feeding on *F. alnus* may be because this plant species provides a small food base, i.e. the leaves and crowns are small and, in relation to other understory species, it occurs rarely.

The results described above support the conclusion that species of shrubs may suffer large leaf damage due to either (or both) a broad diversity of folivorous species being present or a large number of insects from a small number of species being present. Our research omits the variation in speed and amount of leaf tissue mass eaten resulting from the size of insects and their consumption abilities. Accounting for these aspects would require additional research and comparisons. The results described above only partially answer our first question that plant species with a similar degree of leaf damage by folivores and herbivores host a similar species diversity and overall abundance of these herbivores. Our question was only partially explained because depending on the species of the plant, slight or great differences in species diversity (Fig. 6), abundance of specimens (Fig. 7) and similarity of folivorous species (Fig. 2).

### Influence of light conditions on species diversity and abundance of folivores

On several of the plant species we studied, light conditions strongly affected the occurrence of herbivorous insects. Although this applied to the diversity of folivorous species, both dominant and all species, it mainly concerned their abundance. All these factors determined the amount of leaf damage. The strong impact of light was also evidenced by the fact that the variation among plant species regarding leaf damage by insects differed between LL and HL conditions. This variation among species tends to be greater under LL than under HL (Hemming & Lindroth, 1999; Agrell et al., 2000; Karolewski et al., 2013). We have also previously found that, for *C. sanguinea* and *S. nigra*, there is no significant influence of light on leaf damage by insects (Karolewski et al., 2013). Those past results, however, may have occurred because leaf damage in these two species was negligible in general (0 – 5%). In the current study, weak damage on these two plant species corresponded well to the relatively small number of folivores present under both light conditions (Fig. 7).

For some species of plants, the influence of light on the occurrence of folivores, and thus on differences in the extent of leaf damage, is extremely high. The effect can vary greatly, however; i.e. greater sun exposure can result in both more and less damage

caused by herbivores (Roberts and Paul 2006). Differences in damages between LL and HL may be the result of the large influence of light conditions on leaf structure. In *P. serotina*, leaves grown in the sun are leathery, very thick and hard (Mađerek et al., 2015, 2017), and thus the damage they suffer from insects is negligible (Karolewski et al., 2013). This is likely why there were fewer species of folivores on *P. serotina* in HL (Fig. 6A) than in LL (Fig. 6B). Schilthuizen et al. (Schilthuizen et al., 2016) reported that the ratio of the number of herbivorous species on *P. serotina* to those on *P. padus* was 6:4, but there were approximately five times fewer individual herbivores on *P. serotina* than on *P. padus*. The authors did not, however, account for the influence of light in their study. In our research, the number of species of herbivorous insects was similar between both *Prunus* species only under LL conditions, whereas in HL, there were much fewer species on *P. serotina*. Similarly, the abundance of folivores on *P. serotina* shrub leaves in HL was much lower than in LL (ratio of 3:5, HL:LL). In addition, our observations showed that damage to the leaves of both species of *Prunus*, especially *P. serotina*, corresponded mainly to presence of *G. quinquepunctata*. A host choice test carried out by Schilthuizen et al. (Schilthuizen et al., 2016), however, showed that *G. quinquepunctata* does not exhibit a significant preference for *P. serotina*. The inconsistency between those results and our research is difficult to explain based only on the different light conditions where insects were collected. Perhaps the reason for these differences is the variation in species composition of vegetation at the research sites. In general, *P. padus* grows in wetter habitats than *P. serotina*, but in our research, the plants of both species grew in a practically undifferentiated habitat. Other important issues may include differences in time of introduction and the dynamics of *P. serotina* spreading in both areas of research.

For *C. avellana*, different from the majority of other plant species we studied, the leaves of plants growing in HL were more damaged than those in LL, and the ratio of the number of folivores in HL to LL was as much as 25:3.5. In the case of *C. avellana*, light did not appear to have a large impact on leaf structure, although leaves in HL are also harder, and contain more trichomes and defensive compounds than leaves in LL (Łukowski et al., 2015a). For the main pest of *C. avellana*, the monophagous *A. brevicollis coryletorum*, this is likely not an obstacle and does not hinder its feeding. A similar situation was reported by Mooney et al. (Mooney et al., 2009) in the plant *Lindera benzoin* L., where larvae of the specialist *Epicmecis hortaria* Fabricius consumed a greater mass of leaves and achieved greater body mass in HL than in LL. The authors concluded that this difference was due to a larger defensive reaction (the indicator was

peroxidase activity) by leaves in LL than those in HL. We believe that the preference of *A. brevicollis coryletorum* for leaves in HL may be a defence strategy against its predators, as its escape typically involves a rapid jump, which is more effective in HL conditions (warmer temperature) than in LL (Łukowski et al., 2015a). In our research, *C. avellana* growing in HL conditions is the best indicator that the amount of leaf damage may depend not on the number of specimens in the entire species pool of feeding folivores, but rather on the specimen abundance of a single species of insect. Moreover, the dominant polyphagous folivores on *C. avellana* also included *G. quinquepunctata*, but only in the case of shrubs growing in HL. Interestingly, in both HL and LL, we did not observe any specimens of the related *G. pallida* Linnaeus, although according to Axelsson et al. (Axelsson et al., 1973), it is the main pest of hazel in Europe and Scandinavia.

The information described above shows that light conditions have a greater impact on the overall abundance of folivores than on their species diversity. Folivorous insects are more attached to their host plant, and hence similar species diversity was observed under both LL and HL conditions. For each plant species, however, light conditions significantly affected the abundance of herbivorous insects. In general, more herbivores were found on plants growing in LL than on those in HL; *C. avellana* was the exception, with the opposite being true. Correspondingly, in most tested plants, this was indirectly determined by internal factors (leaf structure and chemistry), whereas in *C. avellana*, external factors associated with the light conditions (temperature) likely directly affected the main defoliator (Łukowski et al., 2015a).

### Relationship between leaf damage by insect folivores, and diversity and abundance of predatory arthropods

The amount of leaf damage caused by herbivorous insects on various plant species can be explained relatively well both by the diversity (Table 3, Fig. 6) and the abundance (Fig. 7) of associated zoophages. Defrance et al. (Defrance et al., 1987) found that *S. nigra* is an extremely attractive species for predatory arthropods. In the current study, both species with weak leaf damage (*S. nigra* and *C. sanguinea*) harboured a higher number of species and greater abundance of zoophages than those found on the more damaged *F. alnus* and *P. padus*, but had species diversity and abundance similar to those on *P. serotina*. On *S. nigra*, there were more zoophagous species than herbivores, and on both weakly damaged plants, there was also a significant dominance of zoophagous specimens over herbivores. Perhaps

this is an important cause of minor damage to leaves in these plant species, because the low levels of phenolic compounds and tannins in their leaves cannot protect them from folivores (Karolewski et al., 2013). In contrast, heavily damaged *P. padus*, under both light conditions, exhibited an extremely small ratio of zoophagous species to folivorous species, as well as abundance of specimens.

Like the differences among species of plants, these species' interactions with light conditions can be well explained by the relationships between zoophages and herbivores. On the heavily damaged leaves of *C. avellana* growing in HL, there were more herbivores than zoophages, whereas on the less damaged leaves of plants growing in LL, there were more zoophages than folivores. Furthermore, although the species diversities of folivores and zoophages were relatively large, the difference in species diversity of insects between the light conditions was small. The reason for this is likely the previously described specific defence strategy of the specialist folivore *A. brevicollis coryletorum* (Łukowski et al., 2015a). Additionally, in the case of strongly damaged *P. serotina* growing in LL, the number of herbivores was more than twice large as the number of zoophages, whereas in the case of weakly damaged *P. serotina* growing in HL, the number of folivores was only slightly greater than that of zoophages.

The above examples partially explained the issue of our third question that plants are weakly damaged by insects when there is wide species diversity and a large abundance of zoophages. Our general conclusion is that weak damage likely occurs when there are more zoophagous species than herbivorous species, whereas a plant suffers heavy damage when the opposite is true. The species diversity of folivores or zoophages is less important. Rather, whether generalist or specialist insects are the main cause of damage is more important. In our research, generalists and specialists were represented by *G. quinquepunctata* and *A. brevicollis coryletorum*, respectively. According to Grosman et al. (Grosman et al., 2017) predators follow herbivorous insects to a new host plant slower and to a lesser extent than do parasites. They also concluded that predator movement is a matter of time and in the long run, predators will also adapt to hunting herbivores on a new host plant. The results of our research show that although the enemy-free space hypothesis is likely correct, with such a long time having elapsed since the arrival of *P. serotina* in Europe, escaping from *P. padus* zoophages onto *P. serotina* is less and less effective for folivores (Łukowski et al., 2019). Our qualitative and quantitative data regarding relationships between folivores and zoophages undoubtedly indicate the large role that predatory arthropods play in affecting the degree of leaf damage on certain plants.

## Influence of plant species and light conditions on the occurrence of predatory arthropods

In the case of zoophages, the similarity between species on plants in HL and LL was 63.1% (average of all examined species) – significantly greater than the similarity in zoophages between shrub species (49.3%, average of both light conditions). The greatest similarity in species of zoophages between light conditions was found for *C. sanguinea* and *S. nigra* (ca. 70%), suggesting that in plants most resistant to the feeding of folivores, light conditions have little effect on the species composition of zoophages. There was a relationship between light conditions and the number of predator species (Fig. 6). This was not as evident as in the case of folivores, which may have resulted from the classifying all species of spiders (Araneae) and harvesters (Opiliones) into only two groups, without species divisions. As a result, the total pool of predator species was understated and the differences between LL and HL were reduced. This may have been particularly significant in the case of spiders, which were the dominant group of predators on all six studied plant species. Kytö et al. (Kytö et al., 1996) and Larsson et al. (Larsson et al., 2000) have also shown that the most commonly collected predators are spiders.

On some species of shrubs, there is a strong influence of light on the role of zoophages regarding the amount of damage caused by folivores. In our research, the cases of *C. avellana* and *P. serotina* are the best examples of this influence. The results of our research indicated that more species of zoophages were on plants growing in HL than on those in LL. This may explain the results of Heiling's research (Heiling, 1999) which showed that although spiders are active at night, they build webs during the day in HL places. One of the possible causes could be a better chance of finding folivores in HL areas, due to higher temperatures that improve their moving abilities (e.g. Łukowski et al., 2015).

Differences in the amount of leaf damage among plant species are more closely related to the ratio of folivores to zoophages present on a plant than to species diversity or specimen abundance of zoophages. A high ratio of folivores to zoophages resulted in heavy damage in three species of shrubs (*P. padus* in LL and HL, *P. serotina* in LL and *C. avellana* in HL). In contrast, this ratio was low in *S. nigra* and low leaf damage occurred in both light conditions. On *P. padus*, under both light conditions, there were more than twice as many species and overall specimens of folivores as there were of zoophages, and for *P. serotina*, the number of zoophages was also similar between shrubs growing in HL and LL. Because there are many more folivores in LL than in HL, more zoophages would also be expected in LL.

Instead, the ratio of the number of zoophages to folivores was two times lower in LL than in HL. This likely only resulted, however, from the differences in the number of folivores between light conditions. On weakly damaged leaves of *C. avellana* shrubs growing in LL, the number of zoophage specimens exceeded the number of folivores by several times, whereas on the highly damaged leaves of shrubs in HL, zoophage specimens were fewer than those of folivores.

Overall, these results indicate, that the occurrence of predatory arthropods is associated more strongly with species of plant (i.e. their characteristic composition of folivorous species) than with light conditions. In some plant species, light has a significant effect on presence of zoophages, but mainly indirectly, by affecting the number of individuals.

## Conclusions

Generally, we can conclude that, for both folivores and zoophages, species diversity and overall abundance of individuals are more strongly associated with plant species than with light conditions. The results of our research allow us to provide several conclusions:

- the polyphagous *G. quinquepunctata*, which feeds on the leaves of all examined species, was present in the greatest abundance;
- plant species has a greater impact on species diversity and abundance of insects than does light, for both folivores/herbivores and zoophages;
- there is interaction between species of plant and light conditions, and for some species of plants light affects the abundance of individuals of the abovementioned two groups of arthropods;
- the occurrence of predatory arthropods is associated more strongly with plant species (i.e. their characteristic composition of folivores) than with light conditions;

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