REVIEW

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Parasitoids of the lime leaf miner *Phyllonorycter issikii* (Lepidoptera: Gracillariidae) recorded throughout the area it recently colonized

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Abstract. *Phyllonorycter issikii* (Lepidoptera: Gracillariidae) has recently spread over a considerable part of the Eurasian continent. So far, in Europe, unlike in Russia, it has not significantly affected its food plant (*Tilia cordata*), but its effect may increase over time. The regulating potential of associated parasitoid natural enemies is still low, which probably allows further leaf miner range expansion and population growth. This species is potentially capable of inflicting considerable damage on its host. Therefore, it is important to study its natural enemies, especially their oviposition behaviour and biology. In this paper, we summarize the results of rearing experiments throughout the area it has recently occupied, including our own study in Hungary. Here we list 46 species of parasitoids recorded from *P. issikii*. None of these species are likely to be able regulate the abundance of *P. issikii*. Further studies are needed to determine their effect on the abundance of this host.

INTRODUCTION

The establishment and later range expansion of a species is largely dependent on the regulating efficiency of native enemies in newly colonized areas (Šefrová, 2003; Ermolaev, 2014). A novel host is a new food resource for the local native parasitoids and predators. Predatory species, like oligophagus Hemiptera (Askew & Shaw, 1974; Ermolaev et al., 2011) and parasitoid species start to use the novel species as food. As the native natural enemies begin to shift to the novel host, the local food-web becomes more and more complex (Cornell & Hawkins, 1993, Stone et al., 1995; Schönrogge et al., 1996). The most important mortality factor of leaf miners are hymenopteran parasitoids (Askew & Shaw, 1974, 1979a; Godfray, 1994; Hawkins, 2005). The threshold percentage parasitism for parasitoid regulation of native leaf miner populations is estimated to be 50% (Askew & Shaw, 1979a; Mey, 1991; Szőcs et al., 2013). In contrast, a generally low (less than 25%) effect of native parasitoid assemblages is recorded for invasive leaf miner species such as *Cameraria ohridella* (Deschka et Dimič, 1986) (Freise et al., 2002; Grabenweger et al., 2005; Volter & Kenis, 2006; Matošević & Melika, 2012), *Macrosaccus robiniella* (Clemens, 1959) and *Parectopa robiniella* (Clemens, 1863) (Csóka et al., 2009) and *Phyllonorycter platani* (Staudinger, 1870) (Marković & Stojanović, 2012). Similar patterns are recorded for other species, like *Dryocosmus kuriphilus* (Yasumatsu, 1951) (Hymenoptera: Cynipidae) (Aebi et al., 2007; Matošević & Melika, 2013), though the percentage parasitism of some invaders [*Andricus quercuscalicis* (Burgsdorf, 1783)] has increased over time (Schönrogge et al. 1995).

The factors that determine the number of parasitoid species parasitizing an invasive host have been studied by Cornell & Hawkins (1993). They account for the development of parasitoid assemblages in terms of the effects of residence time, biological characteristics of the introduced species and the host spectrum of the native parasitoids. Similar temporal changes in the species composition of the parasitoids attacking *P. issikii* is to be expected. One important biological characteristic of the host in this respect is its phenology. Grabenweger (2004) found that while parasitoid adults are active in the spring, *C. ohridella* larvae at that time are not suitable for attack. Therefore, the effect of the parasitoid on this leafminer's first generation is very low. According to Marković & Stojanović (2012), the percentage parasitism of the first generation of *P. platani* is also low. Similarly for *M. robiniella* the percentage parasitism of the first generation larvae is also a low (Csóka et al., 2009). In the case of *P. issikii*, larvae of both generations are very similar in terms of the timing of their development to the native *Phyllonorycter* species. However, studies indicate that native parasitoids are not able to regulate the populations of this recently arrived and established species.

Šefrová (2002) reports that the rate of development of the summer generation of *P. issikii* is strongly temperature dependent. Warmer temperatures result in faster development. Yefremova & Mishchenko (2008) predict that the warming climate may allow a third generation to develop. Similar effects associated with climate change are recorded for other insects (Thomson et al., 2010).

The lime leaf miner *Phyllonorycter issikii* (Kumata, 1963)

Phyllonorycter issikii (Kumata, 1963) (Lepidoptera: Gracillariidae) was described in 1963 from its native range, on Hokkaido, Japan. Its wingspan is ca. 6–8 mm. Depending on the autumn mean temperature, it can have two to three generations per year in Central Europe (Perny, 2007) and Middle Volga basin (Yefremova & Mishchenko, 2008). The first generation flies in May–June and the second in August–September, while its mines can be found from July until October (Szabóky & Csóka, 2003; Mészáros & Szabóky, 2005; Perny, 2007; pers. observ.). The tentiform blotch mines are regularly located on the underside of leaves and can generally be found towards the center of the leaf between veins, sometimes at the tip of a leaf (Mészáros & Szabóky, 2005). A single larva develops within each mine. The caterpillar pupates within the mine and the adults overwinter there (Šefrová, 2002).

A summary of its spread is given by Ermolaev (2014). Outside its native range the moth was first found in Korea (Kumata et al., 1983). In Russia (Primorsky territory) it was first observed on *Tilia amurensis* (Ruprecht, 1869) and *Tilia mandshurica* (Ruprecht et Maximowicz, 1856) (Ermolaev, 1977), both of which are native plants. It was found developing well on *Tilia cordata* (Miller, 1768) in 1982 (Yefremova & Mishchenko, 2008). According to Ermolaev (2014), in 1985 the moth reached Moscow. He describes two possible ways in which it might have been introduced into this region: cargo/transport (when the adults were hibernating) and the introduction with the host plant (as ornamental trees planted in parks).

By 2000–2002, the species had spread into the eastern part of Europe (Šefrová, 2002, 2003; Ermolaev & Zorin, 2011, 2012; Ermolaev, 2014) possibly dispersed passively by wind (Šefrová, 2002). The speed of dispersal was estimated by Šefrová (2002) to be at least 110 km/year, and later by Rodeland (2007) as 200 km/year. The current limit to its southern distribution in Europe is Croatia (Matošević, 2007) and Bulgaria (Tomov, 2009), in the east and France (Reinhardt & Rennwald, 2008) and England (Ermolaev, 2014) in the west. It was first reported in the north-eastern part of Hungary in 2003 (Szabóky & Csóka, 2003).

The main damage it causes is considered to be primarily aesthetic, but according to Ermolaev & Zorin (2011) high infestations can result in a decrease the nectar production of lime trees, causing serious economic loss to the honeybee keepers in Russia (Ermolaev & Zorin, 2011) .

P. issikii may have a significant negative effect on the herbivore guild of *Tilia*. As it has become by far the most dominant herbivore species feeding on lime (Segerer, 2008; Jurc, 2012), in many places it may eventually outcompete the native leaf miner species *Stigmella tiliae* (Frey, 1856) and *Bucculatrix thoracella* (Thunberg, 1794).

MATERIAL AND METHODS

We summarized the data in the available literature and two online databases containing host-parasitoid associations: the Universal Chalcidoidea Database hosted by the British Natural History Museum (Noyes, 2015) and the Global Taxonomic Database of Gracillariidae (Lepidoptera), hosted by the Belgian Biodiversity Platform (De Prins & De Prins, 2014).

The dataset for Hungary resulted from our own 4-year rearing project (2011–2014). We collected only mature leaf mines of *P. issikii* from 19 localities throughout Hungary (Szőcs et al., 2014; unpubl.). The mines were cut from the leaves and after a short period of drying were put in air ventilated plastic tubes (in order to avoid the problems with mould) for individual rearing. All the literature data cited in the present work were obtained from similar rearing of individuals and therefore considered comparable.

The parasitoids that emerged were kept in ethanol until identified. We have retained samples for further genetic studies. The results obtained during the first three years are published (Szőcs et al., 2014).

The Shannon diversity index was calculated in order to compare the parasitoid complexes of different hosts, as Matošević & Melika (2012) did in their paper. In order to estimate the significance of the differences in the diversity indexes, we used a two-sample independent t-test.

RESULTS AND DISCUSSION

The species composition of the complex

The presence of the lime leaf miner on the Eurasian continent dates back to the 1970-s. After it spread rapidly local native natural enemies began to parasitize the lime leaf miner. Based on recently published papers 46 parasitoid species have been reared from this leaf miner. A list of the species is presented in Table 1. Forty two of these species belong to the superfamily Chalcidoidea and four to the Braconidae. Members of the Eulophidae are generally associated with leaf miners, especially those of the genus *Phyllonorycter*.

Of the parasitoid species reared in Japan, *Dolichogenidea dilecta* (Haliday, 1834), *Chrysocharis ujiyei* (Kamijo, 1977) (Hirao & Murakami, 2008), *Sympiesis laeviformis* (Kamijo, 1977) and *Pleurotroppopsis japonica* (Kamijo, 1977) are not recorded in other countries parasitizing *P. issikii*. Common species shared with other countries are *Elachertus fenestratus* (Nees, 1834), *Mischotetrastichus petiolatus* (Erdős, 1961), *Pediobius saulius* (Walker, 1839) and *Sympiesis sericeicornis* (Nees, 1834) (Table 1). *Achrysocharoides cilla* (Walker, 1839) and *Sympiesis angustipennis* (Erdős, 1834) are only recorded emerging from this species in Hungary (Szőcs et al., 2014).

In Europe and Russia *Tilia cordata* is the primary host of *P. issikii* (Szabóky & Csóka, 2003; Ermolaev, 2014; Kirichenko, 2014). In natural conditions, it grows as a component of mixed broadleaved forests (Pigott, 1975). Therefore, it might be easy for the native parasitoids to shift to parasitize the novel host.

Based on the data from 14 papers and our own rearing results, the parasitoid species that account for a significant part of lime leaf miner mortality are *Chrysocharis laomedon* (Delucci, 1954), *Cirrospilus elegantissimus* (Westwood, 1832), *Hyssopus geniculatus* (Hartig, 1838), *Minotetrastichus frontalis* (Nees, 1834), *Pnigalio soemius* (Walker, 1839), *Sympiesis sericeicornis* (Nees, 1834) and *Sympiesis gordius* (Walker, 1848) (Table 2). These species are generalist ectoparasitoids with a wide host range and

TABLE 1. The species of parasitoids that have been recorded attacking *P. issikii* in the different areas it has recently colonized. UKR – Ukraine, RUS – Russia, JAP – Japan, BUL – Bulgaria, CRO – Croatia and HUN – Hungary.

	UKR	RUS				JAP						BUL	CRO	HUN
Parasitoid species	Mey, 1991	Ermolaev et al., 2011	Yefremova & Mishchenko, 2008	Yefremova et al., 2009	Yegorenkova et al., 2007	Kamijo, 1965	Kamijo, 1977	Kamijo, 1986	Fry, 1989	Kamijo & Ikeda, 1997	Hirao & Murakami, 2008	Tomov, 2009	Matošević, 2007	Szőcs et al., 2014
BRACONIDAE														
Braconidae sp.														•
Pholetesor sp.											•			
Dolichogenidea dilecta											•			
Apanteles sp.		•	•											•
EULOPHIDAE														
Achrysoscharoides cilla														•
Achrysocharoides sp.											•			
Aprostocetus sp.				•										•
Aprostocetus zoilus (Walker, 1839)					•									•
Chrysocharis laomedon	•	•	•	•										•
Chrysocharis nephereus (Walker, 1839)		•												
Chrysocharis phryne (Walker, 1839)		•												
Chrysocharis pubicornis (Zetterstedt, 1838)		•		•										
Chrysocharis ujiyei (Kamijo, 1977)											•			
Chrysocharis sp.											•			
Cirrospilus sp.											•			
Cirrospilus elegantissimus	•			•										•
Cirrospilus diallus		•	•	•										
Cirrospilus lyncus		•	•	•										•
Cirrospilus pictus	•	•												
Cirrospilus viticola			•	•										•
Cirrospilus vittatus		•												
Dicladocerus westwoodi (Westwood, 1832)		•												
Elachertus sp.											•			
Elachertus fenestratus		•									•			•
Entedon sp.			•											
Hyssopus nigritulus (Zetterstedt, 1838)		•												
Hyssopus geniculatus		•	•	•										
Minotetrastichus frontalis	•	•	•	•	•							•		•
Mischotetrastichus petiolatus		•		•						•				
Neochrysocharis cuprifrons (Erdős, 1954)		•												
Neochrysocharis formosus		•												•
Oomyzus incertus (Ratzeburg, 1844)		•		•										
Pediobius cassidae (Erdős, 1958)				•										
Pediobius metallicus (Nees, 1834)				•										
Pediobius saulius								•						•
Pleurotroppopsis japonica							•							
Pnigalio agraules (Walker, 1839)														•
Pnigalio nemati (Westwood, 1838)		•												
Pnigalio pectinicornis (Linnaeus, 1758)														•
Pnigalio soemius		•	•	•										•
Sympiesis angustipennis														•
Sympiesis dolichogaster (Ashmead, 1888)		•												•
Sympiesis gordius	•	•	•	•										•
Sympiesis laevifrons						•								
Sympiesis sericeicornis	•	•	•	•		•							•	•
PTEROMALIDAE														
Pteromalidae sp.			•											

Table 2. The dominant species of parasitoids of *P. issikii* recorded in the different areas it has recently colonized. • – dominant species, •• – secondary dominant species, ••• – tertiary dominant species. The dominance levels are those cited in the original papers.

Parasitoid species	Ukraine (Mey, 1991)	Russia (Ermolaev et al., 2011)	Russia (Yefremova & Mishchenko, 2008)	Russia (Yefremova et al., 2009)	Bulgaria (Tomov, 2005)	Croatia (Matošević, 2007)	Hungary (Szőcs et al., 2014)
Chrysocharis laomedon		•••	•••	•••			
Cirrospilus elegantissimus	•••						
Hyssopus geniculatus							
Minotetrastichus frontalis			••	••	•		•
Pnigalio soemius		•					
Sympiesis gordius	•	••	•	•			••
Sympiesis sericeicornis	••					•	•••

are frequently recorded in large numbers from other invasive species, such as *C. ohridella* (Freise et al., 2002; Girardoz et al., 2006; Matošević & Melika, 2012), *P. platani* (Mey, 1991; Balázs et al., 2002; Marković & Stojanović, 2012; Matošević & Melika, 2012), *M. robiniella* and *P. robiniella* (Csóka et al., 2009).

It is generally accepted that new resources (i.e. a new host) are primarily exploited by generalist species, which may be more flexible in their host searching behaviour and/or adaptive potential and therefore more able to rapidly exploit a novel host. For example, *S. gordius* is known to be a generalist parasitoid with a broad host range. It is recorded as the dominant regulator of the lime leaf miner in Ukraine by Mey (1991), in the Middle Volga basin in Russia by Yefremova & Mishchenko (2008) and Yefremova et al. (2009) and as a secondary parasitoid by Ermolaev et al. (2011). In Hungary, it was the third most dominant species. The larva of this species is a solitary (only one adult emerges from a mine) larval-pupal ectoparasitoid (Mishchenko & Yefremova, 2012). The female lays an egg close to the host in a mine (Dowden, 1941). After the larva hatches, it kills the host and feeds on its haemolymph. The parasitoid pupa overwinters in the mine (Dowden, 1941). As a syn-ovigenic species, the adult matures eggs during its life time (Jervis et al., 2001, 2003; Ellers & Jervis, 2004), therefore the protein resource obtained from the early stage leafminer larvae is important for the development of eggs (host feeding and stinging behaviour) (Jervis et al., 2008). This behaviour is very common among parasitoids (Askew & Shaw, 1974; Urbaneja et al., 2002; Pinto et al., 2005; Bernardo et al., 2006). Similar behaviour is recorded for *P. soemius*, which is a dominant parasitoid with a significant effect on this host in Russia (Ermolaev et al., 2011). This parasitoid is also a primary (sometimes secondary) solitary ectoparasitoid with a broad host range. According to Bernardo et al. (2006) this species is predator-like in its behaviour: the adult often kills (by stinging) host larvae without feeding (host-feeding) or ovipositing in the mines and its larvae even migrate from one mine to another (Bernardo et al., 2006). Such behavior is hard to quantify in the field. These traits make *P. soemius* one of the most important population control agent in agricultural pest management (Bernardo et al., 2006). *H. geniculatus* is another dominant species of solitary ectoparasitoid (Ermolaev et al., 2011), which overwinters as a pupa (Brockerhoff & Kenis, 1996). This parasitoid was reared only from Russian samples (Ermolaev et al., 2011, 2013). *C. lynchus*, does not play an important role in the regulation of *P. issikii*, but is recorded emerging from this host in almost all the studies carried out in Europe and Russia. *C. lyncus* is a solitary ectoparasitoid, with the ability to behave as a secondary parasitoid. The eggs are laid on the host and the larvae overwinter (Urbaneja et al., 2002). In Hungary (Szőcs et al., 2014), and Bulgaria (Tomov, 2009) as well as in Russia (Yefremova et al., 2009), *M. frontalis* is also one of the main controlling agents of this leaf miner. This species is a gregarious (more than one egg is laid in a mine) ectoparasitoid, whose larvae can behave like a primary, secondary or tertiary parasitoid. The female lays eggs near the host (Yefremova & Mishchenko, 2012) and it overwinters as a last instar larva (Lupi, 2005).

The parasitoids of the invasive *P. issikii* (just as in the case of other invasive species) include more idiobiont than koinobiont species. The more specialized koinobiont parasitoids need to adapt to the novel host's immune system (Pennacchio & Strand, 2006). Therefore, the evolution of a koinobiont parasitoid complex takes longer. This may explain why only a few koinobiont parasitoids emerged from the Hungarian samples of *P. issikii*. In contrast, the parasitoid assemblages associated with native species of leaf miner tend to include more endoparasitoid species (Askew & Shaw, 1979b; Sato, 1990; Szőcs et al., 2013; Yefremova & Kravchenko, 2015). In Russia, where *P. issikii* has been present for longer, *C. laomedon* is an important koinobiont parasitoid (Yefremova & Mishchenko, 2008; Ermolaev et al., 2011; Yefremova et al., 2013), being ranked the third most dominant at every location. As a koinobiont (host remains alive after it is parasitized) the adult lays an egg on the cuticle of a leaf miner larva. After hatching, the larvae leave the caterpillar and start to feed as an ectoparasitoid (Yefremova & Mishchenko, 2012). This species is a primary parasitoid of a large number of leaf miners (De Prins & De Prins, 2014; Noyes, 2015).

In all three places (Europe, Russia and Japan), the parasitoid complexes are diverse and generally composed of parasitoid species known from other *Phyllonorycter* species (Šefrová, 2003; Ermolaev et al., 2011; Matošević & Melika, 2012; Szőcs et al., 2014). Comparisons made between the native parasitoid complexes of *Phyllonorycter* and *P. issikii* (same host family and different host plants)

Table 3. Comparison of the diversity of endo- and ectoparasitoids recorded attacking native and non-native leaf miners in Hungary based on the Shannon diversity index and our own data. * Szőcs et al., 2014; unpubl.; ** Csóka et al., 2009; *** Szőcs et al., unpubl.

Leafminer hosts		Shannon diversity index	
		Endo	Ecto
Invasive	*Phyllonorycter issikii**	0.5	0.7
	*Macrosaccus robiniella***	0.4	0.6
Native	*Phyllonorycter comparella****	0.9	0.7
	*Phyllonorycter roboris****	0.8	0.7

show considerable overlap in the species of parasitoids (Yefremova & Mishchenko, 2008; Matošević & Melika, 2012; Szőcs et al., 2014; Yefremova & Kravchenko, 2015). *M. frontalis* and *A. cilla* that are dominant in Hungary also parasitize non-gracillariid leaf miners, such as *Parna apicalis* (Brischke, 1888) (Hymenoptera: Tenthredinidae) and *Stigmella tiliae* (Frey, 1856) (Lepidoptera: Nepticulidae) living on the same food plant (*T. cordata*) (same food plant, different insect host family) (Szőcs et al., unpubl.).

The proportion of and diversity of ecto- and endoparasitoid species might be a good indicator of the degree of integration of a non-native species into the local fauna. There is no difference in the numbers of ectoparasitoid species parasitizing native and invasive species [based on our own records and those of Csóka et al. (2009)]. In the case of *P. issikii*, the number of ectoparasitoid species is higher than the number of endoparasitoid species (14 ectoparasitoid species to 7 endoparasitoid species) (Szőcs et al., 2014). Two other invasive species (*M. robiniella* and *P. robiniella*) are also parasitized by a lower number of endoparasitoid species than native leaf-miners of the genus *Phyllonorycter*. Shannon diversity indices (Table 3) indicate that the diversity of the ectoparasitoid complex of the invader differ greatly from that of the native species ($t = 5.6569$, $p = 0.0299$, $p < 0.05$; for the two groups native/invasive).

The first native parasitoids to parasitize the novel host were most likely the species with a large host range, which encounter other species of leaf miners of the same genus, *Phyllonorycter*, on adjacent trees. Similar patterns of recruitment of host guild-associated parasitoids are recorded for invasive insect herbivores, for example the cynipid gall wasps on oak (Stone et al., 1995; Schönrogge et al., 1995, 1996) and chestnut (Aebi et al., 2007) in Europe.

Percentage parasitism

Generally the incidence of attacks by parasitoids and predators on invasive species of herbivorous insects is low, at least initially (Schönrogge et al., 1995, 2011; Grabenweger, 2004; Csóka et al., 2009; Marković & Stojanović, 2012; Matošević & Melika, 2012). The reasons are very simple. Initially, the local parasitoid fauna does not “recognize” the invasive species as a possible source of food. Alternatively, the invasive species may have a different life cycle such that native parasitoids are unable to detect the presence of this new food source. Examples include *Cameraria ohridella* (Grabenweger, 2004) and *Parectopa robiniella* (Csóka et al., 2009). In this case, the phenology of the native parasitoids needs to change if they are to track the novel hosts (Cornell & Hawkins, 1993).

The life stages and phenology of *Phyllonorycter issikii* are rather similar to those of native *Phyllonorycter* species. Therefore, it should be easier for the native parasitoids to adapt to this novel host than in case of *C. ohridella* and *P. robiniella.* Csóka et al. (2009) report that the percentage parasitism of *P. robiniella* in Hungary (0.3–15.3%) is much lower than that of *M. robiniella* (varied between 0.3–47.6%) and that this difference is possibly due to differences in their life cycles and phenology and absence of a closely related species of *Parectopa*.

The percentage parasitism of *P. issikii* varies between 0.9% and 37.2% (Table 4) across the area it has recently colonized. These low levels of percentage parasitism indicate that this species is not yet well integrated into the local food-web. Clearly, the effect of native parasitoids is limited, as is the case for other invasive species.

Mortality of leaf miners caused by parasitoids acting as predators is very common, since not only the larvae, but also the adults, feed on host larvae (host feeding, maturation feeding). This behaviour is common among synovigenic species of parasitoids, because they need extra protein to produce more eggs (Flanders, 1950; Godfray, 1994; Jervis et al., 2001; Harvey et al., 2013). The adults attack the first 1–3 instar larvae of *Phyllonorycter*. In fact, more *Phyllonorycter* are killed as a result of host-feeding by adult parasitoids than by parasitism (Askew & Shaw, 1979a, b). After host-feeding, female wasps’ most likely search for oviposition sites close to the feeding location because on heavily infested leaves (mainly in the second generation), mines in different developmental stages can be found. The mortality caused by adult parasitoids as a result of their “maturation“ feeding is usually not included in

Table 4. The percentage parasitism of *P. issikii* recorded in the different areas it has recently colonized.

Country / Location	Source	Rearing time	Parasitation %
Ukraine / Kiev	Mey, 1991	1988	2.9–22.2
Russia / Izhevsk	Ermolaev et al., 2011	2001–2005	0.9–12.5
Russia / Volga basin	Yefremova & Mischcenko, 2008	2006	7–37
Romania	Stolnicu & Ureche, 2007	2006	22.2
Bulgaria	Tomov, 2009	Unknown	13.7–16.1
Hungary	Szőcs et al., 2014; unpubl.	2011–2014	9.6–37.2

estimates of the percentage of hosts killed by these parasitoids. Therefore, the regulating potential of these ectoparasitoids is likely to be considerably greater than previously considered. This is likely to be the most important group of parasitoids of the lime leaf miner, particularly in the early stages of colonization.

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