Invasive leafminers on woody plants: a global review of pathways, impact, and management

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REVIEW

Invasive leafminers on woody plants: a global review of pathways, impact, and management

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Abstract
Leafminers are a taxonomically diverse group of endophagous insects. A number of them are pests in forestry, horticulture and agriculture, and some of them have become important invasive species. Here, we discuss the characteristics of invasive leafminers of woody plants. We first present 12 cases of invasive leaf-mining species belonging to four different insect orders. For each of them, we briefly describe their invasion, including pathways of introduction, their impact and management methods and their ecology. We then discuss various aspects of these invasions. Leafminers are introduced to new continents and spread through various pathways such as horticultural trade and accidental transport of adults and pre-imaginal stages in containers and vehicles. They may also spread long distances with air currents. A few species have serious economic impacts as orchard pests, such as the citrus leafminer, *Phyllocnistis citrella*, or as pests of ornamental plants, such as the horse-chestnut leafminer, *Cameraria ohridella*. The ecological impact of these species should be better studied, especially those killing native trees, such as the birch leaf-mining weevil, *Orchestes fagi*, in Canada. Compared to other insect groups, invasive leafminers are usually recruited by a range of native parasitoids, which may or may not succeed in controlling the invasive species. Biological control by introduction of parasitoids from the native range has often been successful to control invasive leafminers. The review ends by short discussions on taxonomic issues and on the use of leafminers as models to study invasion ecology.

Keywords Leafminers · Woody plants · Invasive species · Pathways · Impact · Biological control

Key message

- Many leaf-mining insects have become invasive pests, and some of them show significant economic and ecological impacts.
- They have been introduced to new continents and spread through various pathways.
- Many have been recruited by native parasitoids, and others have been the target of successful biological control programmes.
- Several invasive leafminers have been erroneously identified during the invasion process.

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Introduction

Insects are among the most numerous invasive species worldwide, and the number of new invasions is increasing exponentially (Seebens et al. 2018), representing a global threat for the economy and the environment (Kenis et al. 2009; Aukema et al. 2011). In Europe alone, about 20 new alien insects are found every year, i.e., about twice as much as four decades ago (Roques 2010). In North America, more than 450 alien insects have colonized forest and urban trees and 14% of these insects cause notable damage to

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trees (Aukema et al. 2010). The majority of these invasive insects are herbivores that have travelled as contaminants on their host plants, and although phytosanitary regulations have become stricter, the live plant trade, in particular for ornamental purpose, remains the main pathway of invasion for insects (Liebhold et al. 2012).

Among invasive herbivore insects, leafminers represent an important group. Many leafminers are known as important economic pests of agricultural crops, whereas others threaten forest and urban plants (Spencer 1973; Digweed et al. 2009; Ellis 2018). Leafminer larvae live inside leaf tissues feeding on the parenchyma or the epidermis, building cavities called mines (Hering 1951). They are known from four insect orders, i.e., Lepidoptera, Hymenoptera, Coleoptera, and Diptera, accounting for more than 10,000 species worldwide (Connor and Taverner 1997). Mines are often species specific and can provide a diagnostic tool for species identification (Hering 1951; Spencer 1976; Ellis 2018). While many species spend their whole larval stage excavating leaf tissue and living in mines, larvae of other species mine in young instars exclusively and then continue their development externally concealed in cases, leaf constructions or freely on leaf surface (Hering 1951). Due to their endophagous lifestyle, leafminers tend to be specific to their host plants, usually at genus level, even though there are many exceptions (Hering 1951; Spencer 1976).

In recent years, leafminers have attracted much attention due to increasing invasion records (Šefrová 2003; Sweeney et al. 2012; van Nieukerken et al. 2012). Many invasive leafminers have colonized important forest, ornamental and orchard trees and shrubs, causing long-lasting outbreaks and serious economic and environmental impacts (Argov and Rössler 1996; Sweeney et al. 2017). Some invasive leafminers have spread very rapidly through an entire continent (Šefrová 2003; Kirichenko et al. 2017a). In addition, leafminers cause concern among the general public because they are easily noticeable, in particular when they affect highly valued ornamental and urban trees (Pocock and Evans 2014).

To our knowledge, invasive leafminers had never been reviewed at a global scale. In this paper, we review invasive leafminers feeding on forest, ornamental and orchard trees, focusing only on those whose larvae feed entirely in mines during the whole larval stage. We briefly describe 12 examples of invasive leafminers of woody plants belonging to four insect orders and discuss their distribution, pathways, impact and management, and various aspects of their invasion ecology. Additionally, we provide a list of invasive leafminers worldwide that are known to be damaging on woody plants (Table 1). The vast majority of the species listed here are invasive in either Europe or North America. This geographic bias reflects the fact that most of the work on invasive tree leafminers has been done in these two continents. It is not clear whether the lack of cases of leafminers invasive on woody plants in other continents, in particular Africa, Asia, and South America, truly results from the absence of leafminer's invasions or whether invasive leaf miners have been overlooked in these regions.

Lepidoptera

The majority of leaf-mining insects belong to Lepidoptera. Species of about 40 families exhibit a large variety of leaf-mining habits (Connor and Taverner 1997; Powell et al. 1997; Ellis 2018). Most leaf-mining moths invasive on woody plants belong to Gracillariidae. Below, we discuss six examples of invasive leaf mining micro-moth, five Gracillariidae, and one recent invasive pest from the family Heliozelidae. Other examples are listed in Table 1.

Cameraria ohridella Deschka and Dimić 1986 (Gracillariidae)

The horse-chestnut leafminer, *C. ohridella,* is one of the best known invasive micro-moths in Europe due to its fast expansion and its spectacular damage on horse chestnut, *Aesculus hippocastanum*, a highly valued and common shade tree in Europe, originating from the Balkans. It was described from Macedonia in the 1980s (Deschka and Dimić 1986). Since then, *C. ohridella* rapidly spread throughout most of Europe, and it is presently found from the UK to western Russia and from Finland to Italy and Spain (De Prins and De Prins 2018).

Its origin has remained unclear for more than two decades. Hypotheses suggested that *C. ohridella* may be a relict of the glacial age, as its host tree (Deschka and Dimić 1986), a non-European leafminer (Grabenweger et al. 2005a), or a species that recently switched from maple species, *Acer* spp., which are occasional hosts (Hellrigl 2001). Molecular studies finally revealed a significant decrease of the moth genetic diversity in most of the Europe compared to the natural stands of horse chestnuts in the Balkan Mountains, suggesting a Balkan origin (Valade et al. 2009). Observations of herbarium material confirmed that the species occurred in natural horse chestnut stands in Albania and Greece at least since 1879 (Lees et al. 2011). However, the reason for its recent and fast spread from the Balkans to the rest of Europe remains a mystery. *Cameraria ohridella* spread via passive transportation of infested leaf fragments and adult moths as stowaways in/on cars, trucks, and other vehicles, as well as via movements of infested seedlings (Gilbert et al. 2004, 2005).

The species damages some but not all species of the genus *Aesculus,* whereas damage on *Acer* spp. is insignificant (Freise and Heitland 2004; D'Costa et al. 2013). It develops most

Table 1 Non-exhaustive list of invasive leafminers worldwide

	Region of origin	Region of introduction	Decade of first invasion	Main host genera	Reference
Lepidoptera—Gracillariidae					
Cameraria ohridella Deschka and Dimić (1986)*	Balkans	Europe	1980	*Aesculus*	Valade et al. (2009)
Macrosaccus robiniella (Clemens 1859)*	North America	Europe	1980	*Robinia*	Davis and De Prins (2011)
Parectopa robiniella Clemens 1863	North America	Europe	1970	*Robinia*	Csóka et al. (2009)
Phyllocnistis citrella Stainton 1856*	Southeast Asia	Worldwide	1990	*Citrus*	CABI 2017
Phyllocnistis vitegenella Clemens 1859	North America	Europe	1990	*Vitis*	Marchesini et al. (2000)
Phyllonorycter blancardella (Fabricius 1781)	Europe	North America	?	*Malus*	Maier (2001)
Phyllonorycter issikii (Kumata 1963)*	East Asia	Palearctic	1980	*Tilia*	Kirichenko et al. (2017a)
Phyllonorycter leucographella (Zeller 1850)*	Medit./West Asia	Europe	1970	*Pyracantha*	Šefrová (2003)
Phyllonorycter mespilella (Hübner 1805)	Europe	North America	?	*Malus, Prunus, Pyrus*	Maier (2001)
Phyllonorycter messaniella (Zeller 1846)	Europe	N. Zealand, Australia	1950	*Quercus, Castanea*	Sinclair and Hughes (2010)
Phyllonorycter platani Staudinger 1870	Balkans to Caucasus	Europe	Nineteenth century	*Platanus*	Šefrová (2001)
Lepidoptera—Heliozelidae					
Antispila oinophylla van Nieukerken et al. (2012)*	North America	Europe	2000	*Vitis*	van Nieukerken et al. (2012)
Lepidoptera—Yponomeutidae					
Argyresthia thuiella (Packard 1871)	North America	Europe	1970	*Thuya, Chamaecyparis*	Konečná and Šefrová (2014)
Coleoptera—Curculionidae					
Isochnus sequensi (Stierlin 1894)	Europe	North America	?	*Salix, Populus*	Sweeney et al. (2012)
Orchestes fagi (Linnaeus 1758)*	Europe	Eastern Canada	2010	*Fagus*	Sweeney et al. (2012)
Orchestes steppensis Korotayev 2016*	Asia	North America	1980	*Ulmus*	Sweeney et al. (2012)
Diptera—Agromyzidae					
Aulagromyza populicola (Walker 1853)	Europe	Canada	1950	*Populus*	Spencer (1973)
Phytomyza ilicis (Curtis 1846)*	Europe	North America	Early twentieth century	*Ilex*	Cameron (1938)

Table 1 (continued)

	Region of origin	Region of introduction	Decade of first invasion	Main host genera	Reference
Hymenoptera – Pergidae					
Phylacteophaga froggatti Riek 1955	Australia	New Zealand	1980	*Eucalyptus*	Faulds (1990)
Hymenoptera—Tenthredinidae					
Fenusa ulmi Sundevall 1847	Europe	North America	Nineteenth century	*Ulmus*	Smith (1971)
Fenusa dohrnii (Tischbein 1846)	Eurasia	North America	Nineteenth century	*Alnus*	Digweed and Langor (2004)
Fenusa pumila Leach 1817*	Eurasia	North America	1920	*Betula*	Digweed et al. (2009)
Fenusella nana (Klug 1816)	Eurasia	North America	1960	*Betula*	Digweed et al. (2009)
Heterarthrus nemoratus (Fallén 1808)	Eurasia	North America	1900	*Betula*	Digweed et al. (2009)
Profenusa thomsoni (Konow 1886)*	Eurasia	North America	1920	*Betula*	Digweed et al. (2009)
Scolioneura betuleti (Klug 1816)*	Eurasia	North America	1980	*Betula*	Digweed et al. (2009)

*Species whose invasion is described in the text

Only species with known records of heavy infestations on trees and whose larvae spend their whole development in the mine are included

? = Decade of first invasion is unknown

commonly two to three generations per year and overwinters in the pupal stage in fallen leaves. *Cameraria ohridella* reached outbreaking densities in many European countries soon after its invasion, causing severe aesthetic damage to horse-chestnut trees (Freise and Heitland 2004). Multivoltinism, high fecundity, and low impact of natural enemies may explain the persistence of high population levels in Europe (Girardoz et al. 2007). However, the moth has a minimal impact on the vigor of its host tree (Salleo et al. 2003). Furthermore, aesthetic damage in summer can be prevented by removing dead leaves in the preceding autumn (Pavan et al. 2003). Stem injection of systemic insecticides is used in some countries to protect highly valued trees (Kobza et al. 2011).

Phyllocnistis citrella Stainton 1856 (Gracillariidae)

The citrus leafminer, *Ph. citrella*, provides an extraordinary example of a global invasion. This species, native to Southeast Asia, started its spread in the 1990s when it was first found in Florida. In less than 20 years, it invaded all citrus production areas worldwide to become a major citrus pest (CABI 2018). Pathways of introduction are not precisely known but the leafminer has often been intercepted on horticultural stock, including on ornamental plants. Larvae can also travel in fruit peel.

Phyllocnistis citrella feeds mostly on *Citrus* spp. (Ellis 2018). The serpentine mines occur mainly on the lower surface of leaves, rarely on the peel of growing fruit (Grafton-Cardwell et al. 2008; Ellis 2018). Larvae pupate inside the mine. The number of generations varies with climatic conditions but can reach 13 in tropical climates (CABI 2018).

Phyllocnistis citrella is an important pest in citrus orchards and ornamental plantations worldwide (CABI 2018). Heavy infestations result in leaf necrosis and drop, decreasing photosynthesis, growth, and fruit production (Schaffer et al. 1997). Citrus nurseries are more affected than mature plantations because young trees are particularly vulnerable (Argov and Rössler 1996). In addition, wounds caused by the leafminer provide an entry port for a number of pathogens, including the invasive Asian bacteria *Xanthomonas axonopodis* pv. *citri,* which cause citrus canker (Graham et al. 2004). The loss of access to international markets due to quarantine issues also had a major economic impact but it is less so now because the leafminer has invaded nearly all possible citrus production areas (CABI 2018).

Considering the importance of *Ph. citrella* as an agricultural pest, various control measures have been developed and applied, including insecticides, the development of resistant varieties, IPM systems based on cultural practices, attract-and-kill methods, and monitoring with pheromone traps (Grafton-Cardwell et al. 2008; Stelinski and Czokajlo 2010; CABI 2018). Insecticides and other control measures have to be applied the whole year (Grafton-Cardwell et al. 2008).

As for many invasive pests, biological control has been widely practiced. Throughout its distribution range, *Ph. citrella* can be attacked by more than 80 hymenopteran parasitoids (Schauff et al. 1998). In the last two decades, several parasitoids were introduced in different parts of the world, with satisfactory results. Examples of successful control include those provided by *Citrostichus phyllocnistoides* in Spain (Garcia-Marí et al. 2004) and *Ageniaspis citricola* in Florida (Hoy et al. 2007).

Phyllonorycter issikii (Kumata 1963) (Gracillariidae)

The lime leafminer, *Ph. issikii,* is a small moth originating from East Asia (Japan, South Korea, and the Russian Far East) (Kumata et al. 1983; Ermolaev 2014) that has recently expanded to the western Palearctic (Šefrová 2002a; Kirichenko 2014). It first appeared in the 1980s in plantations in Moscow (Kozlov 1991) and quickly spread throughout Europe to Belgium (Ermolaev 2014). A phylogeographic study revealed a high genetic diversity in Europe compared to East Asia, suggesting multiple introductions (Kirichenko et al. 2017a). The examination of historical herbarium collections supports the hypothesis of a recent occurrence of a lime-feeding *Phyllonorycter* in the western Palearctic and its long-term presence in East Asia, and particularly in China, from where the insect was not known earlier (Kirichenko et al. 2017b).

The insect is monophagous on lime, *Tilia* spp. It develops one to three generations, the larvae living and pupating in blotch mines. The adults only move over short distances of up to 1 km (CABI 2018). Long-distance dispersal is most probably through plant material or through the transport of adults that hibernate in crevices and other shelters and can be easily carried in containers (Šefrová 2002a).

Phyllorycter issikii is mainly causing aesthetic damage to limes in urban parks and gardens (Šefrová 2002a). It may also affect natural stands, reducing growth (Ermolaev and Zorin 2011). In Western Siberia, the pest threatens vulnerable tertiary relic limes groves, natural monuments, and habitat/species management areas (Kirichenko et al. 2017a). Furthermore, it may have a negative effect on the number of flowers and sugar content in the nectar, reducing honey production (Ermolaev and Zorin 2011). The decline of honey production due to heavy infestations was estimated at 1.12 billion rubles (i.e., about 15 million €) in the Republic of Udmurtiya (western Russia) (Ermolaev and Zorin 2011).

Management methods have not been developed for this pest. Pesticides are not suitable since the insect mainly affects urban trees or stands used for honey production. At least 43 parasitoids species are known in the invaded range against 13 in the native range, but the latter has been much less studied (Szőcs et al. 2015).

Phyllonorycter leucographella (Zeller 1850) (Gracillariidae)

The firethorn leafminer, *Ph. leucographella,* is a species native to Mediterranean Europe and Western Asia. Since the 1970s, it spread toward Northern, Western and Central Europe up to Sweden and the UK, most likely through the trade of ornamental plants (Šefrová 2003; Csóka 2001).

Although larvae can mine many species within the family Rosaceae, its primary host is firethorn, *Pyracantha coccinea*, a popular ornamental shrub in Europe (Walczak et al. 2010). Larvae develop a blotch mine in which they overwinter. Usually, two generations occur per year (Ellis 2018). Damage by the moth is mainly aesthetic.

The invasion ecology of *Ph. leucographella* has been particularly well studied in the UK. Its spread occurred at a velocity of 10.3 km per year, partly through the transport of its host plants (Nash et al. 1995). In less than ten years, the moth recruited 16 native parasitoid species that provided significant control. The size of the parasitoid assemblage was indistinguishable from that of native congeneric species. The most important parasitoids of *Ph. leucographella* were associated with leafminers that had ecological features in common with the invader (Godfray et al. 1995).

Macrosaccus robiniella (Clemens 1859) (Gracillariidae)

Macrosaccus robiniella, previously known as *Phyllonorycter robiniella*, is a North American leafminer that is invasive in Europe (Davis and De Prins 2011). The species was first observed in Switzerland in 1983 and is now found in 23 European countries (De Prins and De Prins 2018). The insect is monophagous on *Robinia* spp. Its main host is the North American black locust, *R. pseudoacacia*, which is widely planted in Europe (Ellis 2018; De Prins and De Prins 2018). The pathway of introduction to Europe is unknown; however, it possibly arrived from North America via the plant trade. Within Europe, the moth probably spread by itself, including through passive wind dispersal, since *R. pseudoacacia* is common along roadsides. However, the spread through the transport of live plants in summer or through the accidental transport of adults in vehicles is also likely. Overwintering occurs at the adult stage, and thus, pupae cannot be transported in dead leaves as in other Gracillariidae (Šefrová 2003; Lees 2010).

Macrosaccus robiniella has two to three generations per year in Europe, forming blotch mines in which it pupates (Šefrová 2002b). When occurring at high densities, damage of this moth may cause premature leaf drop by early or mid-summer (Csóka 2001). *Robinia pseudoacacia* is an important industrial tree species for its fast growth and wood quality in some European countries (Csóka et al. 2009). It is also a good source of nectar for honeybees and a valued ornamental tree (Csóka 2001). Thus, *M. robiniella* has the potential to affect the aesthetic value of the tree and chronic defoliations are likely to impact tree productivity. However, in many European countries, its host tree is also considered as an invasive species because it outcompetes native plants and changes soil chemistry (Lees 2010).

In general, no management method is used against *M. robiniella*. Over 30 European parasitoids have been reported from the pest (Csóka et al. 2009). Parasitism may have a significant impact on the leafminer's populations (Stojanovic and Markovic 2005), with parasitism rates as high as 60% in Italy (Gibogini et al. 1996). All the parasitoid species reared from *M. robiniella* are generalist, developing on native Gracillariidae associated with other woody plant (Csóka et al. 2009).

Antispila oinophylla van Nieukerken et al. 2012 (Heliozelidae)

The grapevine leafminer, *A. oinophylla*, is a species which was not known to science before it invaded another continent and became a pest. The species is native to North America where it has been, for decades, confused with another native leafminer, *Antispila ampelopsifoliella*. In 2006, a new leafminer was recorded in vineyards in Italy in high densities (Baldessari et al. 2009; van Nieukerken et al. 2012). However, at the beginning, the damage was erroneously attributed to a native heliozelid moth, *Holocacista rivillei* (Baldessari et al. 2009; van Nieukerken et al. 2012). In the following years, it was described as a new species, *A. oinophylla,* native to North America and invasive in Italy (van Nieukerken et al. 2012). Since then, *A. oinophylla* has spread to several Italian regions (van Nieukerken et al. 2012; Duso et al. 2013) but has not yet been recorded in other countries.

In its native range, *A. oinophylla* feeds on various plants of the genus *Vitis,* whereas in Italy it has been found on several varieties of grapevine, *V. vinifera* and, occasionally, on *Parthenocissus quinquefolia* (van Nieukerken et al. 2012). It has two generations per year. Larvae overwinter inside an oval case (made of epidermis layers of the mine joined by silk), attached to the vine trunk (van Nieukerken et al. 2012).

The pathway of introduction to Italy remains unknown. Movements of the cases with larvae or pupae attached to traded plants could be a possibility, in particular on ornamental plants. Long-distance transportation of gravid females in containers in air cargo is also possible (van Nieukerken et al. 2012). The presence of several North American haplotypes in Italy suggests that multiple introductions may have occurred (van Nieukerken et al. 2012).

High infestations in commercial vineyards were observed in Italy with up to 100% of the leaves mined in some fields, with an average of 9.5 mines per leaf, suggesting an economic impact, although this latter was not properly assessed (Duso et al. 2013). Insecticides were tested but were not very effective to reduce infestations (van Nieukerken et al. 2012). Natural enemies, including parasitoids, have been observed, but it remains to be seen whether they will be able to control the pest in the medium and long term.

Coleoptera

Leaf-mining habits are observed in at least eight coleopteran families (Connor and Taverner 1997; Ellis 2018) but invasive species on woody plants have been recorded only in the family Curculionidae (weevils) and Buprestidae (jewel beetles). In the last decades, a few Palearctic leaf-mining weevils were recorded in North America (Table 1), and the two most damaging ones are presented below. A European buprestid, *Trachys minutus* L., has recently been recorded from Massachusetts, USA, where it does not seem to cause damage (Westcott and Murray 2012).

Orchestes steppensis Korotayev, 2016 (Curculionidae)

The introduction of the Palearctic elm flea weevil in North America has been a matter of debates. In the 1980s, *Orchestes alni* (L.) was erroneously reported as present in North America, based on incorrect synonymy of *O. alni* and *O. testaceus* (Müller) and confusion of their host plant associations (O'Brien and Wibmer 1982). In fact, these are two different species, the first being a European species feeding on elm, *Ulmus* spp., and the second a Holarctic species feeding on alder, *Alnus* spp. and birch, *Betula* spp. (Sweeney et al. 2012; Pitkin et al. 2018). In 2003, *O. alni* was re-documented in North America (Illinois) and re-identified as a valid taxon based on beetle morphology and its tropic specialization on elms (Anderson et al. 2007). Later on, it was recorded as a serious elm pest in more than 20 American states and Canadian provinces, suggesting that it had been introduced many years before (Looney et al. 2012; Sweeney et al. 2012). However, in 2016, Korotayev (2016) described a new species, *Orchestes steppensis, f*eeding on elm in Russia, Kazakhstan, Mongolia, and China. Based on comparisons with publications on the morphology and biology of the elm flea beetle in North America, he stated that these studies refer to *O. steppensis*, not to *O. alni* (Korotyaev 2016). The identity of the invasive species in North America was confirmed by DNA barcoding (N. Kirichenko, unpublished data).

In its native range, *O steppensis* feeds on Siberian elm, *Ulmus pumila* (Korotyaev 2016). In the twentieth century, this tree has been extensively traded to North America, first to be used as shelterbelts (Wright and Bretz 1949). Then, since it is resistant to Dutch elm disease, it was used in many breeding projects (Leopold 1980). Thus, it is likely that the introduction and spread of the weevil have been due to the large-scale movements of the host tree. In North America, it is found on various *Ulmus* spp. (Looney et al. 2012; Sweeney et al. 2012), but it is particularly damaging to *U. pumila* and hybrid cultivars (Condra et al. 2010). Heavy defoliations have been recorded in Utah, Idaho, Washington, and some other locations across North America (Looney et al. 2012). Most damage is due to the mines that occur very early in the year but also to the adults that directly feed on the leaves. There is only one generation per year and adults overwinter.

No management is presently used against this pest. In China, seven unidentified parasitoid species causing significant parasitism have been obtained, which opens perspectives for biological control in North America (Li et al. 2017).

Orchestes fagi (Linnaeus 1758) (Curculionidae)

The beech leaf-mining weevil, *O. fagi*, is a well-known pest of European beech, *Fagus sylvatica*, in Europe, where cyclic outbreaks occur (Morris 1993; Pitkin et al. 2018). It was first reported on American beech, *Fagus grandifolia*, in Nova Scotia, Canada, in 2012 (Sweeney et al. 2012, 2015). The weevil has one generation per year. Adults overwinter in the litter or under the bark of trees and lay eggs in the very young leaves in spring (Sweeney et al. 2012; Ellis 2018). A precise synchronization of emergence and oviposition of female beetles with bud burst is crucial because young larvae need to feed on very tender leaves. Larvae quickly develop a blotch mine and pupate inside it in a globular cocoon (Ellis 2018). Adults emerge in late spring. While larvae are specific on beech, adults may also feed on other plants (Bale and Luff 1978; Sweeney et al. 2012). However, in Canada, adults feed almost only on beech (Moise et al. 2015).

Since very fresh leaves are damaged at the time most photosynthesis occurs, the impact on trees can be very severe. In Europe, where it may occasionally cause considerable defoliation (Csóka 2003), tree mortality is rare. However, in Eastern Canada, it represents a serious threat to American beech, which is already severely affected by the invasion of the beech scale, *Cryptococcus fagisuga* and the associated beech bark disease, *Nectria coccinea* var. *faginata* (Sweeney et al. 2012). In heavily infested areas in Nova Scotia, the cumulative mortality of American beech increased dramatically, from 20% in 2014 to 97% in 2016 (Sweeney et al. 2017).

Since beech is not traded with leaves across continents, it is unlikely that the weevil arrived with nursery stock. Rather, it most probably travelled as overwintering adults hitchhiking in containers or hidden in any kind of commodity. Within North America, nursery stock, barked logs, lumber, firewood, and bark chips have been cited as potential spread pathways (Sweeney et al. 2012; Morrison et al. 2017).

In the absence of authorized insecticide, the management of the weevil is not easy. The systemic bioinsecticide azadirachtin can be injected to protect highly valuable trees but it is not feasible in forest plantations (Sweeney et al. 2017). A kairomone extracted emitted from beech at the time of budburst, deterpene 9-geranyl-p-cymene, increases catches of males on sticky traps and may be used to monitor populations (Silk et al. 2017). Several parasitoids have been found on *O. fagi* in Europe (Woodcock and Vanbergen 2008;Péré et al. 2011), and the most specific ones could potentially be introduced in North America to lower pest populations and prevent tree mortality.

Diptera

Leaf-mining species are known in at least 14 dipteran families (Connor and Taverner 1997; Ellis 2018). Among them, the family Agromyzidae is the most important, with a considerable number of species, feeding mainly on herbaceous plants (Spencer 1973). Some are global invaders, such as *Liriomyza sativae* (Blanchard), *L. trifolii* (Burgess), and *L. huidobrensis* (Blanchard). These three species are highly polyphagous and have become pests of many agricultural and horticultural plants worldwide, either outdoors or on protected crops (CABI 2018). In contrast, few dipteran leafminers are important pests of woody plants and very few have become invasive (Table 1). Exceptions include *Aulagromyza populicola* (Haliday), a Palearctic species that appeared on *Populus* spp. in Eastern Canada in 1956 (Spencer 1973), and *Phytomyza ilicis* (Curtis), which is described in further details below.

Phytomyza ilicis (Curtis 1846) (Agromyzidae)

The holly leafminer, *Ph. ilicis,* is a tiny fly native to northwestern Europe (Pitkin et al. 2018; Ellis 2018) from where it has spread to other European regions (Csóka 2003). It was accidently introduced into British Columbia (Canada) and Northwest USA in the early twentieth century (Cameron 1938; Spencer 1976). The insect is monophagous on *Ilex* spp. The main host plant in both native and invaded regions is European holly, *Ilex aquifolium,* which is largely used as ornamental in the coastal region of the Pacific Northwest and sold in mass for Christmas decoration (Cameron 1938). As such, the most likely pathway of introduction was the nursery stock trade that in the early twentieth century was poorly regulated. Occasionally, in North America, it can also damage American holly, *Ilex opaca* (Schread 1968).

The fly has only one generation per year. Adults fly in early spring and lay eggs individually in the underside of the petiole or midrib of a young leaf. Larvae live in a blotch mine until March. Although many eggs can be laid in a leaf, usually only one larva develops because of high intraspecific competition (Spencer 1976; Eber 2004).

In the past, infestation rates were rather heavy, with up to 80% of the leaves attacked (Cameron 1938), affecting the ornamental and economic value of the shrub (Spencer 1973, 1976). In the 1930s, five parasitoids were introduced from UK to British Columbia. Four species became established, and two, *Chrysocharis gemma* and *Opius ilicis,* reached high parasitism and had a significant impact on the leafminer's population (McLeod 1962). This biological control program reduced damage to an acceptable level on ornamental plants in parks and gardens but, in commercial nurseries, especially those producing cut branches, the tolerance threshold is much lower, and thus, insecticides are still regularly applied (Dahlsten and Hall 1999).

Hymenoptera

The leaf-mining habit has been observed in four hymenopteran families only: Argidae, Blasticotomidae, Pergidae, and Tenthredinidae. Leaf-mining sawflies of the family Tenthredinidae are the most common ones. They are usually specific to one woody plant genus (Hering 1951; Connor and Taverner 1997; Ellis 2018). Some are notorious invasive species pests (Digweed et al. 2009). In the twentieth century, at least seven leaf-mining sawflies of Palearctic origin were recorded in the Nearctic (Table 1). The invasion of the three most important birch leaf-mining sawflies is described below.

Profenusa thomsoni (Konow 1886) (Tenthredinidae)

The ambermarked birch leafminer, *P. thomsoni,* originates from the Palearctic region and occurs from Western Europe to China and Japan (Zhelokhovtsev 1994; Pitkin et al. 2018). In its native range, it is a rather rare sawfly, mainly found in peat bogs (Schönrogge and Altenhofer 1992). It feeds exclusively on birch, *Betula* spp. Females are parthenogenic, and it has only one generation per year in its entire range. Larvae develop in blotch mines in late summer. The winter is spent as prepupa in a cocoon in the soil (Digweed et al. 1997).

The species was detected in eastern North America in the 1920s, from where it spread to other Canadian provinces and mid-western USA. In the 1970s, it became an important pest of ornamental birch, particularly in Alberta (Digweed and Langor 2004; MacQuarrie et al. 2007). In 1991, it was recorded in Alaska (Snyder et al. 2007). Phylogenetic studies showed no genetic variation in the invaded locations, suggesting a single introduction into North America, possibly via nursery stock and overwintering pupae around plant roots (Digweed and Langor 2004; MacQuarrie et al. 2007). Further dispersal within the continent was likely through the accidental transportation of females from heavily infested urban landscapes (Digweed and Langor 2004).

Until the early 1990s, the sawfly was considered as a serious pest of urban trees. Although it was not killing trees, the numerous mines in later summer caused important aesthetic damage. It was also regularly defoliating natural stands. However, in the 1990s, a parasitoid, previously identified as *Lathrolestes luteolator* and later described as a new species, *L. thomsoni*, suddenly adopted and controlled the pest (MacQuarrie 2008; Soper et al. 2015; Digweed et al. 2009). The origin of the parasitoid is unknown. It is probably a native species that attacks a poorly studied insect although an exotic origin cannot be ruled out (Digweed et al. 2009; Soper et al. 2015). The parasitoid was introduced from Canada to Alaska in 2004-2008 where it contributes to the decline of *P. thomsoni* populations with two other native parasitoids (Soper et al. 2015).

Fenusa pumila Leach 1817 (Tenthredinidae)

The birch leafminer, *F. pumila,* formerly known as *Fenusa pusilla* (Lepeletier), originates from the Palearctic region, where it is found from Europe to Japan (Zhelokhovtsev 1994; Pitkin et al. 2018). In 1923, it was reported from northwest USA and at the same time in many New England states, suggesting that it had been introduced to America long before the date of the discovery (Friend 1933). By 1980, it had expanded widely throughout Canada (Digweed et al. 2009), and in the early 2000s, the species was documented from Alaska (Snyder et al. 2007). The way through which it arrived and spread in North America remains unknown but it is likely through movements of nursery stock and other human transports (Digweed and Langor 2004).

The sawfly produces two to three generations per year, with adults flying from May to September (Digweed et al. 1997). Mature larvae drop to the ground, build a cocoon in the litter, and overwinter as prepupae (Friend 1933). It feeds nearly exclusively on birches, *Betula* spp. (Ellis 2018), but in Europe, it is also occasionally found on alder, *Alnus viridis* (Altenhofer 1980). In the Palearctic, it is a common leafminer, but is rarely recorded at outbreak densities (Ellis 2018), in contrast to North America, where damage on birch, in particular *B. papyrifera* and *B. populifolia*, can be very severe (Digweed et al. 2009). In Canada, the co-occurrence of *F. pumila* and *P. thomsoni*, the first attacking fresh leaves and the second mature leaves, severely and chronically affected the ornamental value of urban birch trees during several decades (Digweed et al. 2009). *Fenusa pumila* also affected tree growth and health in natural stands but such effects have not been quantitatively investigated (Langor et al. 2014). Weakened birch trees are susceptible to other insects, diseases, or abiotic factors that may result in their death.

In the invaded range, *F. pumila* is attacked by 28 native generalist parasitoids but with insignificant impact (Digweed 1998; Digweed et al. 2009). Therefore, biological control programmes were implemented from 1970s to the 2000s in USA and Canada. Four parasitoids from Europe were introduced to North America, and two specific larval parasitoids, the ichneumonids *Lathrolestes nigricollis* and *Grypocentrus albipes,* became established (Langor et al. 2000, Casagrande et al. 2009). These introductions, in particular those of *L. nigricollis*, resulted in a strong decrease in damage levels throughout the introduction range, except in southern New England where outbreaks still occur for unclear reasons (Casagrande et al. 2009).

Scolioneura betuleti (Klug 1816) (Tenthredinidae)

Scolioneura betuleti is another Palearctic birch sawfly in North America. Its introduction is more recent than that of *P. thomsoni* and *F. pumila*. In 1983, it was detected in Ontario, Canada (Digweed and Langor 2004; Snyder et al. 2007). By 2009, the sawfly was detected in four Canadian provinces: Newfoundland and Labrador, Prince Edward Island, Ontario, and Alberta (Digweed et al. 2009).

It has the same life cycle as the two preceding species, with the prepupa overwintering in a cocoon in the soil. In the early literature, this species was considered as bivoltine (Benson 1952). However, in 1980 two putative sibling species were recognized: *Scolioneura betuleti* and *S. vicina* (Altenhofer 1980). They were described as morphologically indistinguishable but as having a different phenology, larvae of *S. vicina* developing from mid-May to mid-July, whereas those of *S. betuleti* occur from August to October (Altenhofer 1980). They both feed on birches, except that *S. betuleti* can also be found on alder, *Alnus viridis.* Although the invasive populations of *S. betuleti* were recorded in Canada feeding on birches in spring, they were all mentioned as *S. betuleti* (Digweed et al. 2009). Molecular genetic studies failed to find genetic divergence between these two sibling species (MacQuarrie et al. 2007), suggesting that they could be considered as one species (Leppänen et al. 2012). In such case, the oldest name *S. betuleti* should be the valid name.

Although severe defoliations have been occasionally observed on ornamental birch, in particular in Alberta, so far, damage levels have not reached those observed for *P. thomsoni* and *F. pumila* (Digweed et al. 2009). Should damage levels increase over time, or should *S. betuleti* invade new, more favorable regions, biological control using parasitoids from the Palearctic region could be considered since leaf-mining sawflies are known to be attacked by specific and highly effective parasitoids, as shown by the successful control of *F. pumila* and *P. thomsoni*.

Discussion

Pathways of introduction and spread

In invasive insects, pathways of introduction are usually not known with precision (Liebhold et al. 2012). In the past, transcontinental movements of leafminers most probably involved the transport of plants or branches. However, nowadays, broadleaved seedlings are usually traded without leaves and soil. Thus, the few recent transcontinental introductions of leafminers probably occurred through other pathways. For example, *O. fagi* possibly arrived from Europe to Canada as adults hidden in containers. *Antispila oinophylla* may have travelled from the USA to Europe as larvae or pupae in cases attached to traded plants or on other substrates. However, within a continent, spread is much easier and may occur in different ways. Firstly, while most adults do not naturally fly very far, spread through air currents should not be neglected, especially with microlepidoptera. Adults can also be transported by vehicles, especially when they swarm at parking places shaded by host trees, as it is the case with *C. ohridella* or *Ph. issikii* (Gilbert et al. 2004; Šefrová 2003). Some species overwinter in dead leaves, which can also be transported by vehicles (Gilbert et al. 2004). However, for many species the main mean of long-distance dispersal is the trade or movement of their host plants. Most invasive leafminers attack ornamental plants, and these are usually moved within continents without control.

Economic and ecological impact of invasive leafminers

Few invasive leafminers of woody plants have had a serious impact on the economy. An exception is *Ph. citrella* that has threatened the citrus industry worldwide. Most invasive leafminers attack ornamental plants, and thus, costs of control measure and tree replacement are usually borne by municipalities and home gardeners. For example, in the early 2000s, the control of *C. ohridella* in Germany cost 10.0 to 33.8 million € per year. The replacement costs for all horse-chestnut trees would be as high as 10.7 billion but this scenario is unrealistic (Reinhardt et al. 2003). It must be noted that trees such as horse chestnuts have a high cultural value and their progressive replacement has a social impact that cannot be easily measured in monetary values (Walter and Binimelis 2009). Some leafminers, such as *Ph. issikii,* may also seriously affect honey production through a decrease in nectar production (Ermolaev and Zorin 2011).

Since hardly any invasive leafminers kill their host trees, and most attack mainly ornamental trees, their ecological impact is probably rather limited. However, *O. fagi* is a notable exception since heavy infestations result in severe tree mortality (Sweeney et al. 2017). More studies should assess the ecological consequences of beech mortality, including through cascading effects on the biodiversity and ecosystem functions in beech ecosystems. Permanent outbreaks of invasive leafminers could also theoretically affect the native fauna through indirect interactions, in particular through apparent competition via natural enemies. Péré et al. (2010a) showed that high populations of *C. ohridella* had a negative influence on populations of native leafminers in the immediate vicinity of horse chestnuts but a subsequent study failed to show the role of apparent competition through shared parasitoids in this effect (Péré et al. 2011).

Recruitment of parasitoids and biological control

Compared to other insect groups, invasive leafminers are well adopted by native parasitoids in the introduction range. This is due to the fact that the majority of leafminers' parasitoids are usually generalists on leafminers sharing similar ecological niches or on taxonomically related hosts. When closely related leafminers occur in the introduction range, the parasitoid assemblage of the invader becomes quickly as furnished as native leafminers, as shown by the introduction of *Phyllonorycter leucographella* and *Phyllonorycter platani* Staudinger in the UK (Godfray et al. 1995) or *M. robiniella* in Europe (Csóka et al. 2009). In some cases, native parasitoids are sufficiently effective to maintain an invasive leafminer under control. Natural control may happen very quickly after invasion, as observed with the leaf-mining moth *Phyllocnistis vitegenella* Clemens, a North American leafminer that invaded vineyards in Europe in the early 1990s and became quickly controlled by native parasitoids (Marchesini et al. 2000). However, it may also happen after several decades of severe damage, as with *P. thomsoni* in Canada (Digweed et al. 2009). In other cases, an abundant parasitoid complex is not sufficient to control the invader. In Central and Western Europe, *C. ohridella* is attacked by dozens of parasitoids without any apparent effect on damage levels (Grabenweger et al. 2010). In North America, 28 native parasitoid species attack the European *Fenusa pumila* at least occasionally, but control was achieved only by the introduction of *L. nigricollis*, a specialist parasitoid from Europe (Digweed et al. 2009). In other cases, when no ecologically or taxonomically closely related species occurs in the introduction range, the parasitoid complex remains poor. For example, in New Zealand, the invasive oak leafminer *Phyllonorycter messaniella* (Zeller) did not recruit any native parasitoid because no *Phyllonorycter* or closely related genera occur in New Zealand and no other leafminer attacks oak. Control was achieved by introducing two parasitoids from Europe that reduced the average levels of attack from 40 + mines per leaf to 2.3 mines (Swan 1973). Classical biological control has been totally or partially successful with a number of invasive leafminers, as described in our review. However, its application has become much stricter in recent years and only natural enemies that are sufficiently specific to prevent nontarget effects on the native fauna are now allowed for introduction (Hajek et al. 2016). In some leafminers, in particular Gracillariidae, finding specific parasitoids may be a challenge. In others, for example, leaf-mining sawflies, the parasitoid complex is often dominated by specialists. In any case, biological control should be considered as an option against invasive leafminers when impact is particularly severe, such as *O. fagi* in Canada.

Overlooked and erroneously identified invasive leafminers

From the 12 invasive leafminers described in the review, at least five were erroneously identified when they first arrived in the introduction range, some being even unknown to science. *Cameraria ohridella* and *A. oinophylla* were described only after they had started invading Europe. *Orchestes steppensis* was two times misidentified when it invaded North America, first as the Holarctic *O. testaceus* and then as the European *O. alni* (Anderson et al. 2007). *Profenusa thomsoni* was erroneously identified in North America twice: first to a local species, *Profenusa alumnata* (Benson 1959), and then to another invasive birch leafminer, *Fenusa pumila*, (Digweed et al. 2009). The taxonomy of the sawfly *S. betuleti* (or *S. vicina*) still remains an unsolved matter.

While taxonomic issues are by no means specific to invasive leafminers, these are particularly prone to such confusions because of their miniature size, morphological and genetic proximity to congeneric species, and insufficient knowledge of their diversity. Accurate species identification and a precise knowledge of their native range are essential to understand their invasion ecology and develop adequate management methods such as biological control. Molecular tools can help solve taxonomic uncertainties and define routes of invasions (Valade et al. 2009; Kirichenko et al. 2017a) and should be integrated with morphological and ecological approaches in invasion ecology.

Invasive leafminers as models in invasion ecology

No matter their pest status, leafminers are excellent models to study biological invasions and test hypotheses in invasion ecology. Indeed, leafminers are particularly easy to sample and can be identified to morphospecies level based on their mines, even when they have left their host plant. Their parasitoids are also easily sampled and reared out. Furthermore, leafminers are good models for citizen science because they can be easily observed and photographed by the general public. As an example, during two decades, *C. ohridella* has been used to study routes of invasion and phylogeography (Valade et al. 2009; Lees et al. 2011), spread mechanisms and spread models (Gilbert et al. 2004, 2005), apparent competition and impact on native species (Péré et al. 2010a, 2010b, 2011), trophic interactions between invasive species and native natural enemies (e.g., Girardoz et al. 2007; Grabenweger et al. 2005a, b, 2010), and citizen science techniques (Pocock and Evans 2014). Besides, leafminers are also commonly used as models by ecologists to study the recruitment of herbivores by alien plants (e.g., Kirichenko et al. 2013; Kirichenko and Kenis 2016). The potential applications of leaf-mining insects to invasion ecology should be further explored.

Author contribution

NK, SA, and MK wrote the manuscript together.

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Compliance with ethical standards

Conflict of interest All authors declare no conflict of interest.

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References

Altenhofer E (1980) Zur Biologie der in Baumblättern minierenden Blattwespen (Hym., Tenthred.). Z Angew Entomol 89:122–134

Anderson RS, O'Brien CW, Salsbury GA, Krauth SJ (2007) *Orchestes alni* (L.) newly discovered in North America (Coleoptera: Curculionidae). J Kans Entomol Soc 80:78–79

Argov Y, Rössler Y (1996) Introduction, release and recovery of several exotic natural enemies for biological control of the citrus leafminer, *Phyllocnistis citrella*, in Israel. Phytoparasitica 24:33–38

Aukema JE, McCullough DG, Von Holle B et al (2010) Historical accumulation of non-indigenous forest pests in the continental United States. BioSci 60:886–897

Aukema JE, Leung B, Kovacs K et al (2011) Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6(9):e24587

Baldessari M, Angeli G, Girolami V et al (2009) *Antispila* sp. minatore fogliare segnalato in Italia su vite. L'Informatore Agrario 15:68–71

Bale JS, Luff ML (1978) The food plants and feeding preferences of the beech leaf mining weevil, *Rhynchaenus fagi* L. Ecol Entomol 3:245–249

Benson RB (1952) Handbooks for the identification of British insects, vol VI Part 2(b). Royal Entomological Society, London

Benson RB (1959) Further studies of the Fenusini (Hymenoptera: Tenthredinidae). Proc R Entomol Soc Lond B 28:90–92

CABI (2018) Invasive Species Compendium. CAB International, Wallingford, UK. www.cabi.org/isc. Accessed 5 Feb 2018

Cameron E (1938) The holly leaf-miner (*Phytomyza ilicis*, Curt.) and its parasites. Bull Ent Res 30:173–208

Casagrande R, Van Driesche RG, Mayer M et al (2009) Biological control of *Fenusa pusilla* (Hymenoptera: Tenthredinidae) in the Northeastern United States: a thirty-four year perspective on efficacy. Fla Entomol 92:243–247

Condra JM, Brady CM, Potter DA (2010) Resistance of landscape-suitable elms to Japanese beetle, gall aphids, and leaf miners, with notes on life history of *Orchestes alni* and *Agromyza aristata* in Kentucky. Arboric Urban For 36:101–109

Connor EF, Taverner M (1997) The evolution and adaptive significance of the leaf-mining habit. Oikos 79:6–25

Csóka G (2001) Recent invasions of five species of leafmining Lepidoptera in Hungary. In: Liebhold AM et al (eds) Proceedings: integrated management and dynamics of forest defoliating insects, 1999 August 15–19, Victoria, BC. Gen. Tech. Rep. NE-277. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, pp 31–36

Csóka G (2003) Leaf mines and leaf miners. Agroinform, Budapest

Csóka G, Pénzes Z, Hirka A et al (2009) Parasitoid assemblages of two invading block locust leaf miners, *Phyllonorycter robiniella* and *Parectopa robiniella* in Hungary. Periodicum biologorum 111:405–411

D'Costa L, Koricheva J, Straw N, Simmonds MSJ (2013) Oviposition patterns and larval damage by the invasive horse-chestnut leaf miner *Cameraria ohridella* on different species of *Aesculus*. Ecol Entomol 38:456–462

Dahlsten DL, Hall RW (1999) Biological control of insects in outdoor urban environments. In: Bellows TS, Fisher TW (eds)

Handbook of biological control: principles and applications. Academic Press, San Diego, New York

Davis DR, De Prins J (2011) Systematics and biology of the new genus *Macrosaccus* with descriptions of two new species (Lepidoptera, Gracillariidae). ZooKeys 98:29–82

De Prins J, De Prins W (2018) Global taxonomic database of gracillariidae (Lepidoptera). http://www.gracillariidae.net/. Accessed 25 Jan 2018

Deschka G, Dimić N (1986) *Cameraria ohridella* sp. n. aus Mazedonien, Jugoslawien (Lepidoptera; Lithocolletidae). Acta Entomol Jugosl 22:11–23

Digweed SC (1998) Mortality of birch leafmining sawflies (Hymenoptera: Tenthredinidae): impacts of natural enemies on introduced pests. Environ Entomol 27:1357–1367

Digweed SC, Langor DW (2004) Distributions of leafmining sawflies (Hymenoptera: Tenthredinidae) on birch and alder in northwestern Canada. Can Entomol 136:727–731

Digweed SC, Spence JR, Langor DW (1997) Exotic birch-leafmining sawflies (Hymenoptera: Tenthredinidae) in Alberta: Distributions, seasonal activities, and the potential for competition. Can Entomol 129:319–333

Digweed SC, MacQuarrie CJK, Langor DW et al (2009) Current status of invasive alien birch-leafmining sawflies (Hymenoptera: Tenthredinidae) in Canada, with keys to species. Can Entomol 141:201–235

Duso C, Baldessari M, Pozzebon A et al (2013) Notes on the biology and the pest status of *Antispila* sp. (Lepidoptera: Heliozelidae) in North-eastern Italy. Integrated Protection and Production in Viticulture. IOBC-WPRS Bull 85:173–176

Eber S (2004) Bottom-up density regulation in the holly leaf-miner *Phytomyza ilicis*. J Anim Ecol 73:948–958

Ellis W (2018) Leafminers and plant galls of Europe. Plant parasites of Europe: leafminers, gallers and fungi. http://bladmineerders.nl/. Accessed 5 Feb 2018

Ermolaev IV (2014) Biological invasion of the lime leafminer *Phyllonorycter issikii* Kumata (Lepidoptera, Gracillariidae) in Europe. Contemp Probl Ecol 7:324–333

Ermolaev IV, Zorin DA (2011) Distribution of the Lime Leafminer *Phyllonorycter issikii* (Lepidoptera, Gracillariidae) in Natural Stands. Entomol Rev 91:1088–1091

Faulds W (1990) Introduction into New Zealand of *Bracon phylacteophagus* a biocontrol agent of *Phylacteophaga froggatti* eucalyptus leaf-mining sawfly. NZ J For Sci 20:54–64

Freise JF, Heitland W (2004) Bionomics of the horse-chestnut leaf miner *Cameraria ohridella* Deschka & Dimić 1986, a pest on *Aesculus hippocastanum* in Europe (Insecta: Lepidoptera: Gracillariidae). Senckenberg Biol 84:1–20

Friend RB (1933) The birch leaf-mining sawfly *Fenusa pumila* Klug. Conn Agric Exp Stn Bull 348:293–364

Garcia-Marí F, Vercher R, Costa-Comelles J, Marzal C, Villalba M (2004) Establishment of *Citrostichus phyllocnistoides* (Hymenoptera: Eulophidae) as a biological control agent for the citrus leafminer Phyllocnistis citrella (Lepidoptera: Gracillariidae) in Spain. Biol Control 29:215–226

Gibogini B, Alma A, Arzone A (1996) Bio-ethological researches on the Hymenoptera of the biocenosis of *Phyllonorycter robiniellus* (Clemens) (Lepidoptera Gracillariidae). Boll Zool Agr Bachic 28:13–22

Gilbert M, Grégoire J-C, Freise JF, Heitland W (2004) Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. J Anim Ecol 73:459–468

Gilbert M, Guichard S, Freise J et al (2005) Forecasting *Cameraria ohridella* invasion dynamics in recently invaded countries: from validation to prediction. J Anim Ecol 45:805–813

Girardoz S, Quicke DLJ, Kenis M (2007) Factors favouring the development and maintenance of outbreaks in an invasive leaf miner *Cameraria ohridella* (Lepidoptera: Gracillariidae): a life table study. Agric For Entomol 9:141–158

Godfray HCJ, Agassiz DLJ, Nash DR, Lawton JH (1995) The recruitment of parasitoid species to two invading herbivores. J Anim Ecol 64:393–402

Grabenweger G, Avtzis N, Girardoz S et al (2005a) Parasitism of *Cameraria ohridella* (Lepidoptera, Gracillariidae) in natural and artificial horse-chestnut stands in the Balkans. Agric For Entomol 7:291–296

Grabenweger G, Kehrli P, Schlick-Steiner B et al (2005b) Predator complex of the horse chestnut leafminer *Cameraria ohridella*: identification and impact assessment. J Appl Entomol 129:353–362

Grabenweger G, Kehrli P, Zweimuller I et al (2010) Temporal and spatial variations in the parasitoid complex of the horse chestnut leafminer during its invasion of Europe. Biol Invasions 12:2797–2813

Grafton-Cardwell EE, Godfrey KE, Headrick DH et al (2008) Citrus leafminer and citrus peelminer. University of California. Division of Agriculture and Natural Resources, Publication, p 8321

Graham JH, Gottwald TR, Cubero J, Achor DS (2004) *Xanthomonas axonopodis* pv. *citri*: factors affecting successful eradication of citrus canker. Mol Plant Pathol 5:1–15

Hajek AE, Hurley BP, Kenis M et al (2016) Exotic biological control agents: a solution or contribution to arthropod invasions? Biol Invasions 18:953–969

Hellrigl K (2001) Neue Erkenntnisse und Untersuchungen über die Roßkastanien-Miniermotte *Cameraria ohridella* Deschka & Dimić, 1986 (Lepidoptera, Gracillariidae). Gredleriana 1:9–81

Hering ME (1951) Biology of the leafminers. Junk's, Gravenhage

Hoy MA, Singh R, Rogers M (2007) Citrus leafminer, *Phyllocnistis citrella* (Lepidoptera: Gracillariidae), and natural enemy dynamics in central Florida during 2005. Fla Entomol 90:358–369

Kenis M, Auger-Rozenberg M-A, Roques A et al (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45

Kirichenko N (2014) The lime leafminer *Phyllonorycter issikii* in Western Siberia: some ecological characteristics of the population of the recent invader. Contemporary Probl Ecol 7:114–121

Kirichenko N, Kenis M (2016) Using a botanical garden to assess factors influencing the colonization of exotic woody plants by phyllophagous insects. Oecologia 182:243–252

Kirichenko N, Péré C, Baranchikov Yu, Schaffner U, Kenis M (2013) Do alien plants escape from natural enemies of congeneric residents? Yes but not from all. Biol Invasions 15:2105–2113

Kirichenko N, Triberti P, Ohshima I et al (2017a) From east to west across the Palearctic: Phylogeography of the invasive lime leaf miner *Phyllonorycter issikii* (Lepidoptera: Gracillariidae) and discovery of a putative new cryptic species in East Asia. PLoS ONE 12(2):e0171104

Kirichenko N, Triberti P, Lopez-Vaamonde C (2017b) Using herbarium data to understand the invasion history of the lime leaf miner *Phyllonorycter issikii* (Gracillariidae) in the Palearctic, Book of abstracts of the 20th European Congress of Lepidopterology. Podgora, Croatia. Croatian Natural History Museum, Zagreb, April 24th—April 30th 2017, p 15

Kobza M, Juhásová G, Adamčíková K, Onrušková E (2011) Tree injection in the management of horse-chestnut leaf miner. *Cameraria ohridella* (Lepidoptera: Gracillariidae). Gesunde Pflanz 62:139–143

Konečná H, Šefrová H (2014) Morphology, biology and control possibilities of two *Argyresthia* species – *A. thuiella* and *A. trifasciata* (Lepidoptera: Argyresthiidae). Acta Univ Agric Silvicult Mendel Brunen 62:529–538

Korotyaev BA (2016) New data on the changes in the abundance and distribution of several species of beetles (Coleoptera) in European Russia and the Caucasus. Entomol Rev 96:620–630

Kozlov MV (1991) Leaf-mining moth is a pest of limes. Plant Protection and Quarantine 4:46

Kumata T, Kuroko H, Park K (1983) Some Korean species of the subfamily Lithocolletinae Gracillariidae, Lepidoptera. Korean J Plant Prot 22:213–227

Langor DW, Digweed SC, Williams DJM et al (2000) Establishment and spread of two introduced parasitoids (Ichneumonidae) of the birch leafminer, *Fenusa pusilla* (Tenthredinidae). Biocontrol (Dordrecht) 45:415–423

Langor DW, Cameron EK, MacQuarrie CJK et al (2014) Non-native species in Canada's boreal zone: diversity, impacts, and risk. Environ Rev 22:372–420

Lees D (2010). *Phyllonycter robiniella* (Clemens 1859) (Lepidoptera, Gracillariidae). In: Roques A et al (eds) Alien terrestrial arthropods of Europe. BioRisk, vol 4, pp 996–997

Lees DC, Lack HW, Rougerie R et al (2011) Tracking origins of invasive herbivores using herbaria and archival DNA: the case of the horse-chestnut leafminer. Front Ecol Environ 9:322–328

Leopold D (1980) Chinese and Siberian elms. J Arboriculture 6:175–179

Leppänen S, Altenhofer E, Liston AD, Nyman T (2012) Phylogenetics and evolution of host-plant use in leaf-mining sawflies (Hymenoptera: Tenthredinidae: Heterarthrinae). Mol Phylogenetics Evol 64:331–341

Li Q, Triapitsyn SV, Wang C, Zhong W, Hu HY (2017) Biological traits and the complex of parasitoids of the elm pest *Orchestes steppensis* (Coleoptera: Curculionidae) in Xinjiang, China. Bull Entomol Res 5:1–10

Liebhold AM, Brockerhoff EG, Garrett LJ et al (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Front Ecol Environ 10:135–143

Looney C, Humble LM, Cranshaw W (2012) *Orchestes alni* (L.) (Coleoptera: Curculionidae): new records from Western North America with notes on Parasitoids. Coleopts Bull 66:63–66

MacQuarrie CJK (2008) Invasion history, population dynamics and biological control of *Profenusa thomsoni* (Konow) in Alaska. University of Alberta, Canada

MacQuarrie CJK, Langor DW, Sperling FAH (2007) Mitochondrial DNA variation in two invasive birch leaf-mining sawflies in North America. Can Entomol 139:545–553

Maier CT (2001) Exotic lepidopteran leafminers in North American apple orchards: rise to prominence, management, and future threats. Biol Invasions 3:283–293

Marchesini E, Posenato G, Sancassani GP (2000) Parassitoidi indigeni della minatrice americana della vite. L'informatore Agrario 10:93–96

McLeod JH (1962) A review of the biological control attempts against insects and weeds in Canada. Part I. Biological control of pests of crops, fruit trees, ornamentals, and weeds in Canada up to 1959. Commonw Inst Biol Control Tech Commun 2:1–33

Moise ERD, Forbes GBH, Morrison A et al (2015) Evidence for a substantial host-use bottleneck following the invasion of an exotic, polyphagous weevil. Ecol Entomol 40:796–804

Morris MG (1993) A review of the British species of Rhynchaeninae (Col., Curculionidae). Entomol Mon Mag 129:177–197

Morrison A, Sweeney J, Hughes C, Johns R (2017) Hitching a ride: firewood as a potential pathway for range expansion of an exotic beech leaf-mining weevil, *Orchestes fagi* (Coleoptera: Curculionidae). Can Entomol 149:129–137

Nash DR, Agassiz DJL, Godfray HCJ (1995) The pattern of spread of invading species: two leafmining moths colonizing Great Britain. J Anim Ecol 64:225–233

O'Brien CW, Wibmer GJ (1982) Annotated checklist of the weevils (Curculionidae sensu lato) of North America, Central America, and the West Indies (Coleoptera: Curculionoidea). Mem Am Entomol Inst vol 34(I-IX), pp 1–382

Pavan F, Barro P, Bernardinelli I, Gambon N, Zandigliacomo P (2003) Cultural control of *Cameraria ohridella* on horsechestnut in urban areas by removing fallen leaves in autumn. J Arboric 29:253–258

Péré C, Augustin S, Tomov R et al (2010a) Species richness and abundance of native leaf miners are affected by the presence of the invasive horse-chestnut leaf miner. Biol Invasions 12:1011–1021

Péré C, Augustin S, Turlings TCJ et al (2010b) The invasive alien leaf miner, *Cameraria ohridella* and the native tree, *Acer pseudoplatanus*: a fatal attraction? Agric For Entomol 12:151–159

Péré C, Bell R, Turlings TCJ, Kenis M (2011) Does the invasive horse-chestnut leaf mining moth, *Cameraria ohridella*, affect the native beech leaf mining weevil, *Orchestes fagi,* through apparent competition? Biodivers Conserv 20:3003–3016

Pitkin B, Ellis W, Plant C, Edmunds R (2018) The leaf and steam mines of British flies and other insects. http://www.ukflymines.co.uk/. Accessed 25 Jan 2018

Pocock MJO, Evans DM (2014) The success of the horse chestnut leafminer, *Cameraria ohridella*, in the UK revealed with hypothesis led citizen science. PLoS ONE 9(1):e86226

Powell JA, Mitter C, Farrell BD (1997) Evolution of larval feeding habits in Lepidoptera. In: Kristensen NP (ed) Handbook for zoology. Lepidoptera, Vol. 1, Systematics and evolution. de Gruyter Publ., Berlin, pp 403–422

Reinhardt F, Herle M, Bastiansen F, Streit B (2003) Economic impact of the spread of alien species in Germany. Federal Environmental Agency (Umweltbundesamt), Berlin

Roques A (2010) Taxonomy, time and geographic patterns. In: Roques A et al (eds) Alien terrestrial arthropods of Europe. Biorisk, vol 4, pp 11–26

Salleo S, Nardini A, Raimondo F et al (2003) Effects of defoliation caused by the leaf miner *Cameraria ohridella* on wood production and efficiency in *Aesculus hippocastanum* growing in northeastern Italy. Trees 17:367–375

Schaffer B, Pena JE, Colls AM, Hunsberger A (1997) Citrus leafminer (Lepidoptera: Gracillariidae) in lime: Assessment of leaf damage and effects on photosynthesis. Crop Prot 16:337–343

Schauff ME, LaSalle J, Wijesekara GA (1998) The genera of chalchid parasitoids (Hymenoptera: Chalcidoidea) of citrus leafminer *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae). J Nat Hist 32:1001–1056

Schönrogge K, Altenhofer E (1992) On the biology and larval parasitoids of the leaf-mining sawlies *Profenusa thomsoni* (Konow) and *P. pygmaea* (Konow) (Hym., Tenthredinidae). Entomol Mon Mag 128:99–108

Schread JC (1968) Leaf miners and their control. Bull Conn Agric Exp Stn 693:3–15

Seebens H, Blackburn TM, Dyer EE et al (2018) The global rise in emerging alien species results from increased accessibility of new source pools. PNAS. https://doi.org/10.1073/pnas.1719429115

Šefrová H (2001) *Phyllonorycter platani* (Staudinger)—a review of its dispersal history in Europe (Lepidoptera, Gracillariidae). Acta Univ Agric Silvicult Mendel Brunen 49:71–75

Šefrová H (2002a) *Phyllonorycter issikii* (Kumata, 1963)—bionomics, ecological impact and spread in Europe (Lepidoptera, Gracillariidae). Acta Univ Agric Silvicult Mendel Brunen 50:99–104

Šefrová H (2002b) *Phyllonorycter robiniella* (Clemens, 1859)—egg, larva, bionomics and its spread in Europe (Lepidoptera: Gracillariidae). Acta Univ Agric Silvicult Mendel Brunen 1:7–12

Šefrová H (2003) Invasions of Lithocolletinae species in Europe–causes, kinds, limits and ecological impact (Lepidoptera, Gracillariidae). Ekologia Bratisl 22:132–142

Silk PJ, Mayo PD, LeClair G, Brophy M, Pawlowski S, MacKay K, Hillier NK, Hughes C, Sweeney JD (2017) Semiochemical attractants for the beech leaf-mining weevil, *Orchestes fagi*. Entomol Exp Appl 164:102–112

Sinclair RJ, Hughes L (2010) Leaf miners: the hidden herbivores. Austral Ecol 35:300–313

Smith DR (1971) Nearctic sawflies III. Heterarthrinae: adults and larvae (Hymenoptera: Tenthredinidae). Agriculture Research Service, US Department of Agriculture, Washington

Snyder C, MacQuarrie CJK, Zogas K, Kruse JJ, Hard J (2007) Invasive species in the last frontier: Distribution and phenology of birch leaf mining sawflies in Alaska. J For 105:113–119

Soper AL, MacQuarrie CJ, Van Driesche R (2015) Introduction, establishment, and impact of *Lathrolestes thomsoni* (Hymenoptera: Ichneumonidae) for biological control of the ambermarked birch leafminer, *Profenusa thomsoni* (Hymenoptera: Tenthredinidae), in Alaska. Biol Control 83:13–19

Spencer KA (1973) Agromyzidae (Diptera) of economic importance, vol 9. Series entomologica. Springer, Berlin, pp 1–405

Spencer KA (1976) The agromyzidae of fennoscandia and Denmark, vol 5, Part 1, 2. Scandinavian science press ltd, Klempenborg

Stelinski LL, Czokajlo D (2010) Suppression of citrus leafminer, *Phyllocnistis citrella* with an attract-and-kill formulation. Entomol Exp Appl 134:69–77

Stojanonovic A, Markovic C (2005) Parasitoid complex of *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera, Gracillariidae) in Serbia. J Pest Sci 78:109–114

Swan DI (1973) Evaluation of biological control of the oak leaf-miner *Phyllonorycter messaniella* (Zell.) (Lep., Gracillariidae) in New Zealand. Bull Entomol Res 63:49–55

Sweeney J, Anderson RS, Webster RP, Nevill R (2012) First records of *Orchestes fagi* (L.) (Coleoptera: Curculionidae: Curculioninae) in North America, with a checklist of the North American Ramphini. Coleopts Bull 66:297–304

Sweeney J, Johns R, Moise E et al (2015) European beech leaf mining weevil: a new invasive established in Nova Scotia. The 26th USDA lnteragency Research Annapolis, Forum on Invasive Species, January 13–16, 2015, Maryland, pp 42–43

Sweeney J, Meating J, Goble T et al (2017) Effect of dosage and treatment frequency of efficacy of TreeAzin® Systematic Insecticide for protecting foliage from the beech leaf-mining weevil and preventing mortality of American beech in high value urban environments. SERG International 2017 workshop. Proceedings, 7-9 Feb 2017. Nat Resour Can Can For Serv 46:1124–1132

Szőcs L, George M, Thuróczy C, Csóka G (2015) Parasitoids of the lime leaf miner *Phyllonorycter issikii* (Lepidoptera: Gracillariidae) recorded throughout the area it recently colonized. Eur J Entomol 112:591–598

Valade R, Kenis M, Hernandez-Lopez A et al (2009) Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive horse-chestnut leaf miner *Cameraria ohridella* (Lepidoptera, Gracillariidae). Mol Ecol 18:3458–3470

van Nieukerken E, Wagner D, Baldessari M et al (2012) *Antispila oinophylla* new species (Lepidoptera, Heliozelidae), a new North American grapevine leafminer invading Italian vineyards: taxonomy, DNA barcodes and life cycle. ZooKeys 170:29–77

Walczak U, Baraniak E, Jerzak E (2010) Host range of an invasive moth, *Phyllonorycter leucographella*. J Appl Entomol 134:714–717

Walter M, Binimelis R (2009) The multiple meanings of the *Cameraria ohridella* biological invasion in Paris's Green Areas. Landscape Res 34:527–544

Westcott RL, Murray TC (2012) An Exotic Leafminer, *Trachys minutus* (L.) (Coleoptera: Buprestidae), found in Massachusetts, U.S.A. Coleopts Bull 66:360–361

Woodcock BA, Vanbergen AJ (2008) Parasitism of the beech leafminer weevil in a woodland: patch size, edge effects and parasitoid species identity. Insect Conserv Divers 1:180–188

Wright E, Bretz TW (1949) Trees—yearbook of agriculture, 1949. Dep. Agric, U.S. Govt. Printing Office, Washington

Zhelokhovtsev AH (1994). Tribe heterarthrini. In: Tobias VI, Zinov'ev AG (eds) Keys to the insects of the European part of the USSR, Vol. III. Hymenoptera, Part IV. Symphyta, EJ Brill, Leiden, Germany, pp 297–318