A checklist of gymnosperm-feeding leafminers (Arthopoda, Insecta) in North America and Europe

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Abstract

The leafminers on gymnosperms receive much less attention than those on either angiosperms or ferns. Given the distinctly different leaf shape and leaf venation found in gymnosperms, they would be expected to host significantly different leafminer groups. Very few comprehensive reports on gymnosperm-feeding leafminers have been presented.

Based on the well-studied fauna in North America and Europe, we compiled a list of 133 species, 30 genera and 13 families of gymnosperm-feeding leafminers. The gymnosperm-mining families (in descending order of leafminer number) included Tortricidae, Gelechiidae, Argyresthiidae, Yponomeutidae, Batrachedridae, Pyralidae, Adelidae, Agromyzidae, Blastobasidae, Bucculatricidae, Coleophoridae, Curculionidae and Noctuidae. There were 109 species, 22 genera and ten families in North America and 34 species, 19 genera and nine families in Europe. We compiled a list of 102 species and 16 genera of host plants, belonging to four families: Pinaceae, Cupressaceae, Taxaceae and Zamiaceae. There were 84 host species, 15 genera and three host families in North America and 46 host species, ten genera and three host families in Europe. Dominant gymnosperm-mining families and dominant host families were generally the same in the two continents.

Keywords

gymnosperm, leafminer, host plant, Pinaceae, Cupressaceae

Introduction

Leafminers are insects that feed inside plant leaves during some or all larval stages, leaving externally visible feeding trails known as leaf mines (Hering 1951, Hespenheide 1991, Dai et al. 2011, Liu et al. 2015, Dai et al. 2018, Yang et al. 2021, Eiseman 2022, Ellis 2022). There are four orders, over 50 families and over 10000 leafminer species worldwide (Csóka 2003, Hirowatari 2009, Liu et al. 2015). Most leafminers are monophagous or oligophagous and different leaf-mining genera or families often have distinct leaf-mine characteristics, which can be helpful for the identification of leafminers (Sinclair and Hughes 2010, Dai et al. 2011, Liu et al. 2015). Moreover, the long-term persistence of leaf mines on either extant or extinct plants can provide a valuable basis for ecologists and paleoecologists to reconstruct life histories and interspecific relationships (Dai et al. 2018, Yang et al. 2021).

Host plants of leafminers encompass nearly all vascular plant groups, including lycophytes, ferns, gymnosperms and angiosperms (Kristensen and Schmidt-Rhaesa 1998, Yang et al. 2021, Eiseman 2022). Unlike the leaves of other plant groups, those of most gymnosperms are needle-like or scale-like, with small leaf areas (Zhang and Gao 2012, Mou et al. 2016, Jacobsen 2021). In addition, leaf veins of many gymnosperms extend to the leaf tips as parallel straight lines and leaf veins of many angiosperms are present as reticulated structures (Boyce 2005, Nicotra et al. 2011). Furthermore, gymnosperms generally have much lower leaf vein densities than angiosperms (Boyce 2008, Boyce 2009, Brodribb and Feild 2010, Brodribb et al. 2010, Nicotra et al. 2011). Small leaves are less likely to be mined than large leaves (Faeth 1991, Low et al. 2009, Dai et al. 2011) and leaf venation patterns may affect the host plant preference and larval feeding paths of leafminers (Ayabe 2010, Dai et al. 2011). Therefore, the leafminers on gymnosperms should be significantly different from those on either typical ferns or angiosperms. Differences between the leafminer faunas of gymnosperms and angiosperms are likely also strongly influenced by phytochemicals, such as secondary metabolites (SMs) (Hespenheide 1991, Dai et al. 2011). Alkaloids, steroids and phenolic acids are less widely distributed in gymnosperms than in angiosperms, while phenypropanoids, lignin and coumarin are more widely distributed in gymnosperms than in angiosperms (Wang 2006, Zhang 2018, Zhang et al. 2020). However, whether these physical and chemical differences shape distinct leafminer groups on gymnosperms and angiosperms requires further investigation.

Compared to angiosperms and ferns (Godfray 1984, Yang et al. 2021), few comprehensive reports on gymnosperm-feeding leafminers have been presented (Eiseman 2022). Therefore, in this study, we compile a checklist of gymnosperm-feeding leafminers and their host plants in North America and Europe, hoping to provide some valuable information on insect-gymnosperm relationships.

Material and methods

Gymnosperm leafminers and their host plants have been more thoroughly studied in North America and Europe than on other continents (Eiseman 2022, Ellis 2022). The information on names and hosts of gymnosperm-feeding leafminers (Suppl. materials 1, 2) was obtained from the book 'Leafminers of North America' (Eiseman 2022), the websites 'Plant Parasites of Europe' (https://bladmineerders.nl) (Ellis 2022) and 'British Leafminers' (http://www.leafmines.co.uk/index.htm) (Edmunds et al. 2022) and a recent publication on conifer-feeding *Batrachedra* species (Berggren et al. 2022). The number of species in each gymnosperm family and the scientific names, authorships and publication years for insect species were compiled from the website 'Catalogue of Life' (https://www.catalogueoflife.org/) (Hobern et al. 2021).

Note that the book 'Leafminers of North America' covers only miners that occur in the continental US and Canada (Eiseman 2022), so some species that occur only in Mexico or the Caribbean may be missed. The website 'Plant Parasites of Europe' includes records from ornamental and crop plants, but excludes those from indoor ornamentals, greenhouse plants, uncommon ornamentals, exotics in botanical gardens and cultivars (Ellis 2022). Some host plants have been recorded only at the genus level, especially in the European datasets (Edmunds et al. 2022, Eiseman 2022, Ellis 2022). To be consistent in these cases, we use "spp." after a genus name to indicate one or more unknown host plant species in this genus. However, such cases are uncommon in the above sources.

In our checklist, both non-native leafminers and non-native host plants for the respective biogeographical regions are included. For example, *Thuja* and *Pseudotsuga* are not native to Europe, but they were also incorporated into the host plants of European gymnosperm-feeding leafminers and *Spilonota laricana*, a European moth introduced in North America, is listed for both continents (Eiseman 2022, Ellis 2022). The insect species that feed as leafminers only for part of their larval development (e.g. *Coleotechnites carbonaria*, *C. gibsonella*) are also included (Eiseman 2022, Ellis 2022). Insects, whose status as leafminers is uncertain and plants that require confirmation as hosts for a given leafminer, are marked with a question mark (?) before their scientific name in Table 1 and Suppl. materials 1, 2. Such insects and plants are included in the statistics. However, insect species without full scientific names (i.e. undescribed species) and those without definite host records to at least the plant genus level (e.g. *Rhyacionia blanchardi*, *R. pallifasciata*, *R. salmonicolor* and *R. versicolor*) are excluded (Eiseman 2022). Such cases are uncommon in the above sources.

There are several parasitic modes of gymnosperm-feeding insects, including miner, borer, galler etc. (Brown 2018, Eiseman 2022, Ellis 2022). Species with parasitic modes, other than leaf-mining, were not included in this study, unless they feed as leafminers in early instars. Bark-mining species (e.g. *Spulerina corticicola* (*De Prins and De Prins 2022*), *Marmara fasciella*, *M. oregonensis* and other undetermined *Marmara* species (

Fitzgerald 1975, Eiseman 2022), were excluded from this study, as were species with unknown parasitic modes.

Results

In total, there were 133 species, 30 genera and 13 families of gymnosperm-feeding leafminers in the two continents, with 109 species, 22 genera and ten families in North America and 34 species, 19 genera and nine families in Europe, with only ten leafminer species occurring in both North America and Europe (Table 1). The leaf-mining families were Tortricidae, Gelechiidae, Argyresthiidae, Yponomeutidae, Batrachedridae, Pyralidae, Adelidae, Agromyzidae, Blastobasidae, Bucculatricidae, Coleophoridae, Curculionidae and Noctuidae (Table 1).

In Tortricidae, there were 53 species and 12 genera of gymnosperm-feeding leafminers with 64 host plant species and nine host genera, including 43 leafminer species with 58 host species, eight host genera and two host families in North America and 12 leafminer species with 13 host species, six host genera and two host families in Europe (Table 2). Amongst tortricid genera, *Rhyacionia* and *Epinotia* were the two richest in gymnosperm-feeding leafminer species. There were 19 leafminer species and 21 host species in *Rhyacionia* and 13 leafminer species and 19 host species in *Epinotia.* Whereas *Epinotia* was recorded in both North America and Europe, *Rhyacionia* was recorded only in North America. Amongst tortricid species, *Archips packardiana*, with 15 host species, was the leafminer with the most host species and was recorded only in North America (Table 1). *Archips oporana*, with six host species, was the leafminer with the second most host species and was recorded only in Europe (Table 1).

In Gelechiidae, there were 42 species and four genera of gymnosperm-feeding leafminers with 50 host plant species and ten host genera, including 41 leafminer species with 45 host species, ten host genera and two host families in North America and four leafminer species with ten host species, five host genera and two host families in Europe (Table 2). Amongst gelechiid genera, *Coleotechnites* is the richest in gymnosperm-feeding leafminer species, with 33 leafminer species in North America, but only one species in Europe.

In Argyresthiidae, there were 20 species and one genus of gymnosperm-feeding leafminers with 28 host plant species and eight host genera, including 14 leafminer species with 13 host species, seven host genera and two host families in North America and eight leafminer species with 22 host species, five host genera and two host families in Europe (Table 2). All of these insects belong to the genus *Argyresthia* (Table 2).

In Yponomeutidae, there were seven species and three genera of gymnosperm-feeding leafminers with 22 host plant species and one host genus, including four leafminer species with 17 host species, one host genus and one host family in North America and four leafminer species with seven host species, one host genus and one host family in Europe (Table 2). Amongst yponomeutid genera, *Ocnerostoma* is the richest in

gymnosperm-feeding leafminer species, with four leafminer species and seven host species.

Of all these leafminers, just one polyphagous species (*Liriomyza schmidti*) is presumed to feed on both gymnosperms and angiosperms and it is also the only gymnosperm-mining dipteran fly in our study. The other 132 species (i.e. > 99%) feed exclusively on gymnosperms.

For host plants, there were 102 species, 16 genera and four families represented in the two continents. Eighty-four species, 15 genera and three families were found in North America, including Pinaceae, Cupressaceae and Zamiaceae (Table 3). Forty-six species, ten genera and three families were found in Europe, including Pinaceae, Cupressaceae and Taxaceae (Table 3).

In Pinaceae, there were 74 host species, six host genera and 102 associated leafminer species, including 65 host species, six host genera and 83 leafminer species in North America and 29 host species, five host genera and 26 leafminer species in Europe (Table 3). Amongst gymnosperm genera, *Pinus* was richest in both host species and leafminer species, with 38 host species and 67 leafminer species, including 35 host species and 59 leafminer species in North America and eight host species and ten leafminer species in Europe.

In Cupressaceae, there were 26 host species, eight host genera and 32 associated leafminer species, including 18 host species, eight host genera and 25 leafminer species in North America and 16 host species, four host genera and ten leafminer species in Europe (Table 3). Amongst gymnosperm genera, *Juniperus* was second richest in host species and fourth richest in leafminer species, with 14 host species and 22 leafminer species, including nine host species and 15 leafminer species in North America and nine host species and nine leafminer species in Europe (Table 3).

In North America, gymnosperm-feeding leafminers belong to ten families, mostly in Tortricidae (43 species, 39.45%), Gelechiidae (41 species, 37.61%), Argyresthiidae (14 species, 12.84%), Yponomeutidae (four species, 3.67%) and Pyralidae (two species, 1.83%) (Table 2, Fig. 1a). In Europe, gymnosperm-feeding leafminers belong to nine families, mostly in Tortricidae (12 species, 35.29%), Argyresthiidae (eight species, 23.53%), Gelechiidae (four species, 11.76%), Yponomeutidae (four species, 11.76%) and Batrachedridae (two species, 5.88%) (Table 2, Fig. 1b).

There were two orders and two classes of host plants for gymnosperm-feeding leafminers in the two continents, including the orders of Pinales (class Pinopsida) and Cycadales (class Cycadopsida) (Table 3). Almost all host plants belong to the order Pinales, with just one belonging to the order Cycadales (Table 3).

In North America, there were three families and two orders of host plants, including Pinales (Pinaceae and Cupressaceae) and Cycadales (Zamiaceae) (Table 3). In Europe, there were three families of host plants, all belonging to the order Pinales, including Pinaceae, Cupressaceae and Taxaceae (Table 3). Pinaceae had the largest number of

host species in both North America and Europe, but with different genera having the most host species. In North America, the genus *Pinus* (35 host species) of Pinaceae had the most host species (Table 3), while the genera *Abies* (nine host species) of Pinaceae and *Juniperus* (nine host species) of Cupressaceae had the most host species in Europe (Table 3).

Discussion

In this paper, we provide a list of the known gymnosperm-feeding leafminers and their host plants in North America and Europe. Here, we give a brief overiew of gymnosperm-mining families in the two continents, in descending order of species richness:

(1) Tortricidae (junior synonym: Olethreutidae) (Lepidoptera). Insects within this family are able to feed on many plant parts, usually as leaf-rollers or borers, with some inducing galls (Brown 2018, Eiseman 2022, Ellis 2022). Only a few tortricid species have mining behaviour (Ellis 2022). Most of these are not typical leafminers, with the mining behaviour occurring only in early instars and older larvae feed as borers in other plant parts or externally in leaf shelters (Eiseman 2022, Ellis 2022). It should be noted here that species of *Rhyacionia*, which we have reported to be the tortricid genus richest in gymnosperm leaf-mining species, feed primarily as shoot borers. The few *Rhyacionia* species for which detailed life history information is available all feed initially as leafminers and the rest are only assumed to do so (Eiseman 2022). On the other hand, several *Epinotia* species do mine in leaves of Pinaceae throughout their development (Eiseman 2022). Many tortricid species are conifer-feeding specialists (Brown 2018). For example, the leaf-mining species *Choristoneura fumiferana* feeds exclusively on Pinaceae (Eiseman 2022) and is an important pest of coniferous forest trees in North America (Brown 2018). The number of leafminer species in this family was greatest amongst all mining families of gymnosperms in both North America and Europe (Table 2).

(2) Gelechiidae (Lepidoptera). Host plants of this family are extremely diverse, with more than 80 host families utilised (Kristensen and Schmidt-Rhaesa 1998). Only a small proportion of gelechiid species have mining behaviour (Kristensen and Schmidt-Rhaesa 1998) and, as with Tortricidae, many of them do so only in early instars (Eiseman 2022). The larvae of several gelechiid genera feed on gymnosperms and three of these (*Coleotechnites, Exoteleia* and *Chionodes*) include species that feed exclusively on Pinaceae (Brown 2018). One needle-mining *Coleotechnites* species was first observed on *Pinus jeffreyi* in southern California in 1963, but remains undescribed (Luck 1976, Eiseman 2022).

(3) Argyresthiidae (Lepidoptera). This family includes about 160 species worldwide (Eiseman 2022). The larvae usually feed on host plants as miners or as borers in buds, flowers, seeds, fruit, cones or twigs (Eiseman 2022). In total, 42% of species feed on conifers as leafminers (Powell 1980, Brown 2018). Over 13 families of plants are utilised by larvae of the genus *Argyresthia* (gymnosperms and dicots) (Kristensen and Schmidt-Rhaesa 1998). However, there is no record of larvae of this genus feeding on

angiosperms as leafminers, with the exception of an erroneous report of the willow-feeding species *A. pygmaeella* doing so (it is in fact a shoot- and catkin-borer) (Eiseman 2022).

(4) Yponomeutidae (Lepidoptera). At least 18 plant families are utilised by yponomeutid moths, including gymnosperms (Pinaceae) and angiosperms (e.g. Betulaceae, Celastraceae and Rosaceae) (Ulenberg 2009). Most yponomeutid species are external feeders on leaves (Kristensen and Schmidt-Rhaesa 1998) and only a few are leafminers (Eiseman 2022). The larvae of three yponomeutid genera feed on gymnosperms (Eiseman 2022, Ellis 2022). Amongst the pine needle-mining *Ocnerostoma* species is one that feeds on *Pinus resinosa* and remains undescribed (Freeman 1960, Maier et al. 2011). *Zelleria haimbachi* is another *Pinus*-mining specialist (Brown 2018, Eiseman 2022); when nearly mature, the larvae move more freely and web around the needle bases (Eiseman 2022).

(5) Batrachedridae (Lepidoptera). This is a small family of tiny moths, with only a few species feeding as leafminers (Ellis 2022). In North America, just two species are known to feed as leafminers (*Batrachedra concitata* on *Agave* and *B. pinicolella* on *Abies*) (Eiseman 2022). Two gymnosperm-mining batrachedrid species occur in Europe and one of these (*B. pinicolella*) has recently invaded North Amercia (Maier 2005, Berggren et al. 2022).

(6) Pyralidae (Lepidoptera). The larvae of pyralid moths have diverse types of feeding behaviour. Some act as leaf-tiers or leaf-rollers, others as borers in stems, cambium or fruit and still others even feed on dead plant material (Eiseman 2022, Ellis 2022). Only a few pyralid species are leafminers, with very few feeding on gymnosperms (Eiseman 2022, Ellis 2022). In North America and Europe, just two species are gymnosperm-feeding leafminers (*Pococera robustella* and *Dioryctria reniculelloides*), with both mining leaves only in early instars (Eiseman 2022, Ellis 2022).

(7) Adelidae (Lepidoptera). This is a small and relatively primitive family (Kozlov and Robinson 1996) with about 350 species (Hobern et al. 2021). Many adelid species are leafminers in their early instars (Kozlov and Robinson 1996). Just one species (*Nemophora associatella*) is recorded as an *Abies*-feeding leafminer in Europe (Ellis 2022).

(8) Agromyzidae (Diptera). This is a family widely distributed throughout the world (Mujica and Kroschel 2011) and it is one of the largest fly families (Civelek 2003, Dousti 2010). It is well-known for diverse leafminers, some of which are economically important (Benavent-Corai et al. 2005). About half of agromyzid species are leafminers (Ellis 2022). The genus *Liriomyza* alone has more than 300 leaf-mining species (Mujica and Kroschel 2011). More than ten agromyzid genera have mining behaviour in North America alone, but just one species is known to be a gymnosperm-feeding leafminer (Eiseman 2022). *Liriomyza schmidti* is an extremely polyphagous species with reported hosts in nearly 30 families, one of which is the cycad family Zamiaceae (Eiseman 2022).

No agromyzid species is recorded as a gymnosperm-feeding leafminer in Europe (Ellis 2022).

(9) Blastobasidae (Lepidoptera). This is a relatively small moth family with a wide distribution around the world (Karsholt and Sinev 2004, Ellis 2022). Most blastobasid larvae are detritus feeders (Ellis 2022). Conifer-feeding blastobasids are cone feeders or external webbers (Brown 2018) and there are six pine-feeding specialists in the genus *Holcocera* (Brown 2018). Just one blastobasid species (*Blastobasis vittata*) is a gymnosperm leafminer in Europe, occasionally mining in yew (*Taxus baccata*) or spruce (*Picea* sp.) as young larvae (Ellis 2022).

(10) Bucculatricidae (Lepidoptera). This family has a wide distribution around the world (Vargas and Mundaca 2016, Tokár and Laštůvka 2018). Most bucculatricid species are leafminers in their early instars, while a few species are gallers (Vargas and Mundaca 2016). *Bucculatrix inusitata* is reportedly a Cupressaceae specialist (Brown 2018), but this is based on a single specimen that is labelled as having been reared from a larva on *Juniperus* (Braun 1963). This host record requires confirmation, since *Bucculatrix* larvae commonly wander from their food plants before spinning cocoons and *B. inusitata* belongs to a group of species that otherwise are virtually all Asteraceae specialists (Braun 1963). No other Bucculatricidae have been reported from gymnosperms in North America or Europe (Eiseman 2022, Ellis 2022).

(11) Coleophoridae (Lepidoptera). Virtually all coleophorid larvae begin their lives as leafminers or within ovules and seeds and, at later larval stages, live in portable silk cases, from which the leaf-mining species continue to make fleck mines (Eiseman 2022, Ellis 2022). In North America and Europe, there is just one gymnosperm-mining species (*Coleophora laricella*), which is native to Europe and was introduced in North America in the 1800s (Eiseman 2022, Ellis 2022).

(12) Curculionidae (Coleoptera). This family has a wide distribution around the world (Wikipedia 2022) and it is the largest beetle family (Bandeira et al. 2021), but only a small proportion of curculionid species are leafminers (Ellis 2022). Thirty-one species and eight genera in Curculionidae are leafminers in North America, none of them feeding on gymnosperms (Eiseman 2022). However, one curculionid species (*Brachonyx pineti*) has been recorded as a gymnosperm-feeding leafminer in Europe (Ellis 2022).

(13) Noctuidae (Lepidoptera). This is amongst the largest moth families (Ellis 2022). Many noctuid larvae are external feeders or borers in either stems or roots (Eiseman 2022, Ellis 2022), while only several species have mining behaviour (Eiseman 2022). First instars of a single North American species (*Feralia jocosa*) have been observed to mine into *Tsuga* needles, although they do not fully enter the needles as with typical miners (Eiseman 2022). No noctuid species mine gymnosperms in Europe (Ellis 2022).

In both North America and Europe, leafminer groups on angiosperms are extraordinarily diverse, followed by those on gymnosperms, while those on ferns and their allies are the least (Suppl. material 3; Yang et al. 2021, Eiseman 2022, Ellis 2022). Amongst the

leafminers on either ferns or angiosperms, Lepidoptera has the most leaf-mining families (Yang et al. 2021, Eiseman 2022, Ellis 2022). Similarly, 11 of the 13 gymnosperm-feeding families belong to Lepidoptera (Table 2). In contrast with angiosperms and ferns, gymnosperms host just one leaf-mining beetle (Coleoptera), one leaf-mining fly (Diptera) and no leaf-mining sawfly (Hymenoptera) species (Table 1). Several leafminer families such as Noctuidae, Curculionidae and Agromyzidae occur in all three vascular plant groups (Yang et al. 2021, Eiseman 2022, Ellis 2022). Agromyzidae is a family best known as leafminers (Spencer 1990). Curculionidae has many leafminer species, but Noctuidae has only a few (Eiseman 2022). Whereas ferns and angiosperms host many specialised leafmining families (e.g. Gracillariidae, Agromyzidae, Anthomyiidae, Tischeriidae, Acanthopteroctetidae, Nepticulidae, Heliozelidae, Bedelliidae, Lyonetiidae, Elachistidae) (Kristensen and Schmidt-Rhaesa 1998, Yang et al. 2021, Eiseman 2022), virtually none of the leafminers of gymnosperms belongs to specialised leafmining families, with the exception of a single extremely polyphagous agromyzid that is believed to be responsible for mines found on Cycadales. It is worth mentioning that, although there are no leafmining gracillariid species on gymnosperms in North America or Europe, there are bark-miners in the genus *Marmara* (e.g. *M. fasciella* and *M. oregonensis*) (Eiseman 2022). However, the focus of this study is on leaf-mining species.

Some insect families, known for their leafmining habits, are absent or rare on gymnosperms (e.g. Tischeriidae, Nepticulidae, Gracillariidae and Agromyzidae). Worldwide, no species of Tischeriidae (Kristensen and Schmidt-Rhaesa 1998, Xu et al. 2021, Alipanah et al. 2022) or Nepticulidae (Powell 1980, Kristensen and Schmidt-Rhaesa 1998, Menken et al. 2009, Doorenweerd et al. 2015) are recorded as leafminers on gymnosperms; both families occur only on angiosperms. In Gracillariidae, although most larvae are leafminers (at least during their early instars) (Eiseman 2022, Ellis 2022), no gracillariid leafminer is recorded on gymnosperms in either North America or Europe (Suppl. material 3; Eiseman 2022, Ellis 2022). However, two gracillariid leafminers are known to feed on gymnosperms in other regions (see below) (Liu et al. 2018, De Prins and De Prins 2022). Agromyzidae, another well-known leafmining family, has many leafminer species on angiosperms, ferns and even bryophytes, but only *Liriomyza schmidti* is recorded from a gymnosperm and this association has yet to be confirmed by rearing (Spencer 1990, Yang et al. 2021, Eiseman 2022, Ellis 2022).

Generally, North America is richer in gymnosperm leafminers than Europe (species 109:34; genus 22:19; family 10:9) (Table 2). The higher diversity of leafminers found in North America is probably correlated with higher availability of potential host plants. North America has a larger species number and distribution area of gymnosperm hosts than Europe (Fragnière et al. 2015). For example, cycads exist in the Rocky Mountain and Caribbean regions in North America, but not in Europe (Fragnière et al. 2015). In North America, gnetophytes are distributed in the Caribbean regions, Mexico and the vast regions of the US, while in Europe, there are just a few distributed near the southern coast (Fragnière et al. 2015). Although conifers occur in almost all regions of North America (ca. 330 species) and Europe (ca. 100 species), their species number and

distribution area in North America is larger (Flora of North America Editorial Committee 1993, Euro+Med 2006, Fragnière et al. 2015).

Leaf-mining insects are greatly affected by leaf features of host plants, including leaf size, leaf thickness, leaf venation and leaf phytochemicals (Hespenheide 1991, Dai et al. 2011). Differences in these features may explain why gymnosperms and angiosperms have significantly different leafminer species. On the other hand, gymnosperms with leaf features similar to those of angiosperms may have correspondingly similar leafminer groups. *Gnetum* (Gymnospermae: Gnetaceae) is a representative example, with a leaf type closely approximate to that of angiosperms (Spencer 1990, Stewart et al. 1993). Therefore, it is a suitable host candidate for Agromyzidae (Spencer 1990), which is a common leafminer family on angiosperms. Cycads likewise share some herbivorous insect species with angiosperms (Whitaker and Salzman 2020). The palm-like leaves of the cycad *Zamia integrifolia* (Zamiaceae) might explain why it is an acceptable host for the polyphagous species *Liriomyza schmidti*, which otherwise is only known to feed on angiosperms (Eiseman 2022). Gracillariidae is a well-known leafminer family, but just two species have been found to feed in leaves of gymnosperms (the Japanese *Phyllocnistis podocarpa* mines in *Podocarpus macrophyllus* (Podocarpaceae) and in New Zealand *Parectopa leucocyma* mines in *Agathis australis* (Araucariaceae)) (Liu et al. 2018, De Prins and De Prins 2022). This may also be related to the unusual leaf morphology of the host plants. Unlike most conifer species with leaves in the form of scales or needles, podocarps have larger, bilaterally flattened leaves and vein reticulation (Brodribb 2011). Similarly, compared with other typical gymnosperms, the leaves of the genus *Agathis* are more broad and flattened with rounded tips (Stockey 1982). Therefore, the distinctive leaf structure of host plants may cause the gracillariid leafminers to mine selectively on gymnosperms. Podocarpaceae and Araucariaceae are sister families (Quinn et al. 2002), implying that plant phylogeny and phytochemistry might also play a role in determining the presence/absence of leafminers on plants.

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Conflicts of interest

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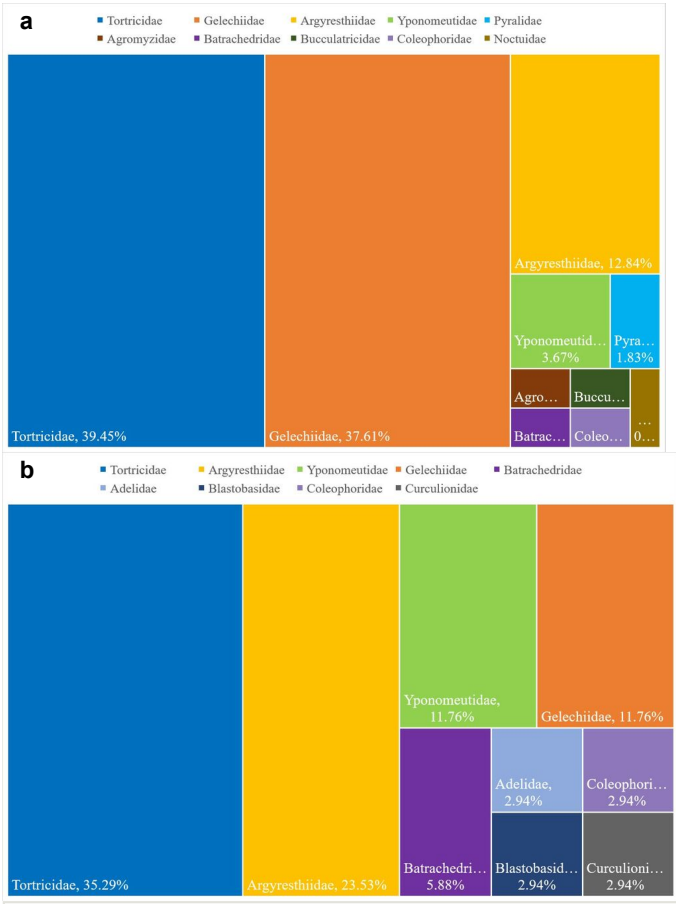

Figure 1.

Percentage distribution of the gymnosperm-mining species in different insect families.

a: North America

b: Europe

Table 1.

A checklist of gymnosperm-feeding leafminers in North America and Europe.

Miner family	Miner species	Host plants	Distribution Region
Lepidoptera			
Adelidae	*Nemophora associatella* Zeller, 1839	*Abies alba*	Europe
Argyresthiidae	*Argyresthia abdominalis* Zeller, 1839	*Juniperus communis*	Europe
Argyresthiidae	*Argyresthia affinis* Braun, 1940	*Juniperus virginiana*	North America
Argyresthiidae	*Argyresthia annettella* Busck, 1907	*Juniperus communis*	North America
Argyresthiidae	*Argyresthia arceuthobiella* Busck, 1917	*Calocedrus decurrens*	North America
Argyresthiidae	*Argyresthia aureoargentella* Brower, 1953	*Thuja occidentalis*	North America
Argyresthiidae	*Argyresthia aurulentella* Stainton, 1849	*Juniperus communis*, *Juniperus foetidissima*	Europe
Argyresthiidae	*Argyresthia canadensis* Freeman, 1972	*Thuja occidentalis*	North America
Argyresthiidae	*Argyresthia cupressella* Walsingham, 1890	*Chamaecyparis* spp., *Cupressus* spp., *Juniperus* spp., *Sequoia sempervirens*, *Thuja* spp.	North America, Europe*
Argyresthiidae	*Argyresthia dilectella* Zeller, 1874	*Chamaecyparis* spp., *Juniperus communis*, *Juniperus sabina*	Europe
Argyresthiidae	*Argyresthia flexilis* Freeman, 1960	*Pinus flexilis*	North America
Argyresthiidae	*Argyresthia franciscella* Busck, 1915	*Cupressus macrocarpa*	North America
Argyresthiidae	*Argyresthia freyella* Walsingham, 1890	*Juniperus virginiana*	North America
Argyresthiidae	*Argyresthia fundella* Fischer von Röslerstamm, 1835	*Abies alba*, *Abies balsamea*, *Abies concolor*, *Abies grandis*, *Abies nordmanniana*, *Abies numidica*	Europe
Argyresthiidae	*Argyresthia libocedrella* Busck, 1917	*Calocedrus decurrens*, *Chamaecyparis lawsoniana*	North America
Argyresthiidae	*Argyresthia pilatella* Braun, 1910	*Pinus radiata*, ?*Pinus torreyana*	North America
Argyresthiidae	*Argyresthia reticulata* Staudinger, 1877	*Juniperus communis*	Europe
Argyresthiidae	?*Argyresthia thoracella* Busck, 1907	*Juniperus* spp.	North America

Argyresthiidae	*Argyresthia thuiella* Packard, 1871	*Chamaecyparis lawsoniana*, *Cupressus* spp., *Thuja occidentalis*, *Thuja plicata*	North America, Europe*
Argyresthiidae	*Argyresthia trifasciae* Braun, 1910	*Cupressus macrocarpa*	North America
Argyresthiidae	*Argyresthia trifasciata* Staudinger, 1871	*Chamaecyparis lawsoniana*, *Cupressus* x *leylandii*, *Juniperus chinensis*, *Juniperus horizontalis*, *Juniperus sabina*, *Juniperus squamata*, *Juniperus virginiana*, *Juniperus* x *media*, *Thuja occidentalis*	Europe
Batrachedridae	*Batrachedra confusella* Berggren, Aarvik, Huemer, Lee et Mutanen, 2022	*Pinus sylvestris*	Europe
Batrachedridae	*Batrachedra pinicolella* Zeller, 1839	*Abies* spp., *Picea abies*, *Picea glauca*, *Picea pungens*, *Picea rubens*, *Pinus* spp.	North America*, Europe
Blastobasidae	*Blastobasis vittata* Wollaston, 1858	*Picea* spp., *Taxus baccata*	Europe
Bucculatricidae	*Bucculatrix inusitata* Braun, 1963	?*Juniperus communis*	North America
Coleophoridae	*Coleophora laricella* Hübner, 1817	*Larix decidua*, *Larix gmelinii*, *Larix kaempferi*, *Larix laricina*, *Larix occidentalis*, *Larix sibirica*, *Pseudotsuga menziesii*	North America*, Europe
Gelechiidae	*Chionodes electella* Zeller, 1839	*Abies alba*, *Abies pinsapo*, *Juniperus communis*, *Picea abies*	Europe
Gelechiidae	*Chionodes retiniella* Barnes & Busck, 1920	*Pinus ponderosa*, *Pinus sabiniana*, *Tsuga heterophylla*	North America
Gelechiidae	*Coleotechnites albicostata* Freeman, 1965	*Juniperus virginiana*	North America
Gelechiidae	*Coleotechnites apicitripunctella* Clemens, 1860	*Tsuga canadensis*	North America
Gelechiidae	*Coleotechnites ardas* Freeman, 1960	*Pinus contorta* var. *latifolia*	North America
Gelechiidae	*Coleotechnites atrupictella* Dietz, 1900	*Abies balsamea*, *Abies grandis*, *Abies lasiocarpa*, *Picea engelmannii*, *Picea glauca*, *Picea mariana*, *Picea rubens*, *Picea sitchensis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Tsuga heterophylla*	North America
Gelechiidae	*Coleotechnites biopes* Freeman, 1960	*Pinus contorta* var. *latifolia*	North America
Gelechiidae	*Coleotechnites blastovora* McLeod, 1962	*Picea glauca*	North America
Gelechiidae	*Coleotechnites canusella* Freeman, 1957	*Pinus banksiana*, *Pinus contorta* var. *latifolia*	North America
Gelechiidae	*Coleotechnites carbonaria* Freeman, 1965	*Juniperus* spp.	North America
Gelechiidae	*Coleotechnites condignella* Busck, 1929	*Pinus ponderosa*	North America

Gelechiidae	*Coleotechnites coniferella* Kearfott, 1907	*Pinus banksiana*	North America
Gelechiidae	*Coleotechnites ducharmei* Freeman, 1962	*Picea glauca*, *Picea mariana*, *Picea rubens*	North America
Gelechiidae	*Coleotechnites edulicola* Hodges & Stevens, 1978	*Pinus edulis*	North America
Gelechiidae	*Coleotechnites florae* Freeman, 1960	*Pinus contorta* var. *latifolia*	North America
Gelechiidae	*Coleotechnites gibsonella* Kearfott, 1907	*Juniperus communis*	North America
Gelechiidae	*Coleotechnites granti* Freeman, 1965	*Abies grandis*	North America
Gelechiidae	*Coleotechnites juniperella* Kearfott, 1903	*Juniperus communis*	North America
Gelechiidae	*Coleotechnites laricis* Freeman, 1965	*Larix laricina*	North America
Gelechiidae	*Coleotechnites lewisi* Freeman, 1960	*Pinus flexilis*	North America
Gelechiidae	*Coleotechnites macleodi* Freeman, 1965	*Tsuga canadensis*	North America
Gelechiidae	*Coleotechnites martini* Freeman, 1965	*Picea abies*, *Picea glauca*	North America
Gelechiidae	*Coleotechnites milleri* Busck, 1914	*Pinus contorta* var. *murrayana*	North America
Gelechiidae	?*Coleotechnites moreonella* Heinrich, 1920	?*Pinus ponderosa*, *Pinus ponderosa* var. *scopulorum*	North America
Gelechiidae	*Coleotechnites obliquistrigella* Chambers, 1872	*Juniperus virginiana*	North America
Gelechiidae	*Coleotechnites occidentis* Freeman, 1965	*Juniperus scopulorum*	North America
Gelechiidae	*Coleotechnites piceaella* Kearfott, 1903	*Abies balsamea*, *Picea abies*, *Picea glauca*, *Picea mariana*, *Picea omorika*, *Picea pungens*, *Picea rubens*	North America, Europe*
Gelechiidae	*Coleotechnites pinella* Busck, 1906	*Pinus ponderosa*	North America
Gelechiidae	*Coleotechnites ponderosae* Hodges & Stevens, 1978	*Pinus ponderosa*	North America
Gelechiidae	*Coleotechnites resinosae* Freeman, 1960	*Pinus banksiana*, *Pinus resinosa*	North America
Gelechiidae	*Coleotechnites* sp.	*Pinus jeffreyi*	North America
Gelechiidae	*Coleotechnites stanfordia* Keifer, 1933	*Cupressus macrocarpa*	North America

Gelechiidae	*Coleotechnites starki* Freeman, 1957	*Pinus contorta* var. *latifolia*	North America
Gelechiidae	*Coleotechnites thujaella* Kearfott, 1903	*Thuja occidentalis*	North America
Gelechiidae	?*Coleotechnites variiella* Chambers, 1872	*Taxodium distichum*	North America
Gelechiidae	*Dichomeris marginella* Fabricius, 1781	*Juniperus* spp.	North America*, Europe
Gelechiidae	*Exoteleia anomala* Hodges, 1986	*Pinus ponderosa*	North America
Gelechiidae	*Exoteleia burkei* Keifer, 1932	*Pinus attenuata*, *Pinus coulteri*, *Pinus radiata*, *Pinus sabiniana*	North America
Gelechiidae	*Exoteleia chillcotti* Freeman, 1963	*Pinus palustris*	North America
Gelechiidae	*Exoteleia dodecella* Linnaeus, 1758	*Larix decidua*, *Pinus banksiana*, *Pinus mugo*, *Pinus nigra*, *Pinus resinosa*, *Pinus strobus*, *Pinus sylvestris*, *Pinus uncinata*	North America*, Europe
Gelechiidae	*Exoteleia nepheos* Freeman, 1967	*Pinus mugo*, *Pinus resinosa*, *Pinus sylvestris*	North America
Gelechiidae	*Exoteleia pinifoliella* Chambers, 1880	*Pinus banksiana*, *Pinus echinata*, *Pinus palustris*, *Pinus pungens*, *Pinus resinosa*, *Pinus rigida*, *Pinus sylvestris*, *Pinus taeda*, *Pinus virginiana*, ?*Pinus contorta*, ?*Pinus ponderosa*	North America
Noctuidae	*Feralia jocosa* Guenée, 1852	*Abies balsamea*, *Abies grandis*, *Abies lasiocarpa*, *Larix laricina*, *Larix occidentalis*, *Picea mariana*, *Picea engelmannii*, *Picea glauca*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Tsuga canadensis*, *Tsuga heterophylla*, *Tsuga mertensiana*	North America
Pyralidae	*Dioryctria reniculelloides* Mutuura & Munroe, 1973	*Abies* spp., *Larix* spp., *Picea engelmannii*, *Picea glauca*, *Picea mariana*, *Picea pungens*, *Picea sitchensis*, ?*Picea rubens*, ?*Pinus contorta*, *Pseudotsuga menziesii*, *Tsuga heterophylla*	North America
Pyralidae	*Pococera robustella* Zeller, 1848	*Pinus banksiana*, *Pinus echinata*, *Pinus elliottii, Pinus mugo*, *Pinus palustris*, *Pinus resinosa*, *Pinus rigida*, *Pinus strobus*, *Pinus sylvestris*, *Pinus taeda*, *Pinus virginiana*	North America
Tortricidae	*Aethes rutilana* Hübner, 1817	*Juniperus* spp.	North America
Tortricidae	*Archips oporana* Linnaeus, 1758	*Abies alba*, *Juniperus communis*, *Larix decidua*, *Picea abies*, *Pinus sylvestris*, *Thuja occidentalis*	Europe
Tortricidae	*Archips packardiana* Fernald, 1886	*Abies amabilis*, *Abies balsamea*, *Abies lasiocarpa*, *Larix* spp., *Picea abies*, *Picea engelmannii*, *Picea glauca*, *Picea mariana*, *Picea pungens*, *Picea rubens*, *Picea sitchensis*, *Pinus banksiana, Pinus contorta*, *Tsuga canadensis*, *Tsuga heterophylla*	North America

Tortricidae	*Argyrotaenia occultana* Freeman, 1942	*Abies balsamea*, *Larix laricina*, *Picea engelmannii*, *Picea glauca*, *Picea mariana*, *Picea rubens*, *Pinus contorta*, *Pseudotsuga menziesii*, *Tsuga* spp.	North America
Tortricidae	*Argyrotaenia pinatubana* Kearfott, 1905	*Pinus strobus*	North America
Tortricidae	*Argyrotaenia tabulana* Freeman, 1944	*Pinus albicaulis*, *Pinus banksiana*, *Pinus contorta* var. *latifolia*, *Pinus ponderosa*	North America
Tortricidae	*Choristoneura carnana* Barnes & Busck, 1920	*Abies concolor*, *Pseudotsuga macrocarpa*, *Pseudotsuga menziesii*	North America
Tortricidae	*Choristoneura fumiferana* Clemens, 1865	*Abies balsamea*, *Larix laricina*, *Picea glauca*, *Picea rubens*, *Pinus* spp.	North America
Tortricidae	*Choristoneura houstonana* Grote, 1873	*Juniperus ashei*, *Juniperus californica*, *Juniperus chinensis*, *Juniperus scopulorum*, *Juniperus virginiana*, ?*Juniperus occidentalis*, ?*Juniperus osteosperma*, *Juniperus virginiana*	North America
Tortricidae	*Choristoneura lambertiana* Busck, 1915	*Abies* spp., *Pinus* spp.	North America
Tortricidae	*Choristoneura occidentalis* Freeman, 1967	*Abies* spp., *Picea* spp.	North America
Tortricidae	*Choristoneura orae* Freeman, 1967	*Abies amabilis*, *Picea sitchensis*	North America
Tortricidae	*Choristoneura pinus* Freeman, 1953	*Pinus* spp.	North America
Tortricidae	*Choristoneura retiniana* Walsingham, 1879	*Abies concolor*, *Abies grandis*, *Abies magnifica*	North America
Tortricidae	*Choristoneura spaldingana* Obraztsov, 1962	*Abies concolor*	North America
Tortricidae	*Clavigesta purdeyi* Durrant, 1911	*Pinus contorta*, *Pinus nigra*, *Pinus sylvestris*	Europe
Tortricidae	*Cymolomia hartigiana* Ratzeburg, 1840	*Abies alba*, *Picea abies*	Europe
Tortricidae	*Dichelia histrionana* Frölich, 1828	*Abies alba*, *Picea abies*	Europe
Tortricidae	*Epinotia aridos* Freeman, 1960	*Pinus contorta* var. *latifolia*	North America
Tortricidae	*Epinotia balsameae* Freeman, 1965	*Abies balsamea*	North America
Tortricidae	*Epinotia fraternana* Haworth, 1811	*Abies alba*, *Abies cephalonica*, *Abies grandis*, *Abies nordmanniana*	Europe
Tortricidae	*Epinotia hopkinsana* Kearfott, 1907	*Picea sitchensis*, *Pinus* spp.	North America
Tortricidae	*Epinotia meritana* Heinrich, 1923	*Abies concolor*, *Abies magnifica*	North America
Tortricidae	*Epinotia nanana* Treitschke, 1835	*Abies alba*, *Picea abies*, *Picea glauca*, *Picea mariana*, *Picea pungens*, *Picea rubens*, *Picea sitchensis*	North America*, Europe

Tortricidae	*Epinotia normanana* Kearfott, 1907	*Picea abies*, *Picea glauca*, *Picea pungens*, *Picea rubens*	North America
Tortricidae	*Epinotia pusillana* Peyerimhoff, 1863	*Abies alba*	Europe
Tortricidae	*Epinotia pygmaeana* Hübner, 1799	*Abies alba*, *Picea abies*, *Picea sitchensis*	Europe
Tortricidae	*Epinotia subsequana* Haworth, 1811	*Abies alba*, *Abies grandis*, *Picea abies*	Europe
Tortricidae	*Epinotia tedella* Clerck, 1759	*Picea abies*	Europe
Tortricidae	*Epinotia trossulana* Walsingham, 1879	*Abies concolor*, *Abies magnifica*, ?*Pseudotsuga menziesii*	North America
Tortricidae	*Epinotia tsugana* Freeman, 1967	*Abies amabilis*, *Picea sitchensis*, *Tsuga heterophylla*, *Tsuga mertensiana*	North America
Tortricidae	*Pseudohermenias abietana* Fabricius, 1787	*Abies alba*, *Picea abies*	Europe
Tortricidae	*Rhyacionia adana* Heinrich, 1923	*Pinus banksiana*, *Pinus resinosa*, *Pinus sylvestris*	North America
Tortricidae	?*Rhyacionia aktita* Miller, 1978	*Pinus elliottii*, *Pinus rigida*, *Pinus taeda*	North America
Tortricidae	*Rhyacionia buoliana* Denis & Schiffermüller, 1775	*Pinus banksiana*, *Pinus densiflora*, *Pinus mugo*, *Pinus nigra*, *Pinus palustris*, *Pinus ponderosa*, *Pinus resinosa*, *Pinus rigida*, *Pinus strobus*, *Pinus sylvestris*, *Pinus thunbergii*, *Pinus virginiana*	North America
Tortricidae	?*Rhyacionia busckana* Heinrich, 1923	*Pinus ponderosa*, *Pinus resinosa*, *Pinus sylvestris*	North America
Tortricidae	?*Rhyacionia bushnelli* Busck, 1914	*Pinus banksiana*, *Pinus nigra*, *Pinus ponderosa*, *Pinus resinosa*, *Pinus sylvestris*	North America
Tortricidae	*Rhyacionia frustrana* Comstock, 1880	*Pinus echinata*, *Pinus elliottii*, *Pinus palustris*, *Pinus ponderosa*, *Pinus radiata*, *Pinus resinosa*, *Pinus rigida*, *Pinus strobus*, *Pinus sylvestris*, *Pinus taeda*, *Pinus virginiana*	North America
Tortricidae	?*Rhyacionia fumosana* Powell & Miller, 1978	*Pinus ponderosa*	North America
Tortricidae	?*Rhyacionia granti* Miller, 1985	*Pinus banksiana*	North America
Tortricidae	?*Rhyacionia jenningsi* Powell, 1978	*Pinus ponderosa*	North America
Tortricidae	?*Rhyacionia martinana* Powell, 1978	?*Pinus edulis*	North America
Tortricidae	?*Rhyacionia monophylliana* Kearfott, 1907	*Pinus monophylla*	North America
Tortricidae	?*Rhyacionia multilineata* Powell, 1978	*Pinus ponderosa*	North America

Tortricidae	?*Rhyacionia neomexicana* Dyar, 1903	*Pinus ponderosa*	North America
Tortricidae	?*Rhyacionia pasadenana* Kearfott, 1907	*Pinus contorta*, *Pinus muricata*, *Pinus radiata*	North America
Tortricidae	?*Rhyacionia rigidana* Fernald, 1880	*Pinus echinata*, *Pinus resinosa*, *Pinus rigida*, *Pinus taeda*, *Pinus virginiana*	North America
Tortricidae	?*Rhyacionia sonia* Miller, 1967	*Pinus banksiana*	North America
Tortricidae	?*Rhyacionia subcervinana* Walsingham, 1879	*Pinus jeffreyi*, *Pinus ponderosa*	North America
Tortricidae	?*Rhyacionia subtropica* Miller, 1961	*Pinus elliottii*, *Pinus palustris*, *Pinus taeda*	North America
Tortricidae	?*Rhyacionia zozana* Kearfott, 1907	*Pinus contorta*, *Pinus jeffreyi*, *Pinus ponderosa*	North America
Tortricidae	*Spilonota laricana* Heinemann, 1863	*Larix aricina*, *Larix decidua*, *Larix kaempferi*, *Picea sitchensis*	North America*, Europe
Tortricidae	*Taniva albolineana* Kearfott, 1907	*Picea abies*, *Picea engelmannii*, *Picea glauca*, *Picea mariana*, *Picea pungens*, *Picea rubens*, *Picea sitchensis*	North America
Yponomeutidae	*Cedestis gysseleniella* Zeller, 1830	*Pinus contorta*, *Pinus mugo*, *Pinus nigra*, *Pinus nigra subsp. Laricio*, *Pinus sylvestris*	Europe
Yponomeutidae	*Cedestis subfasciella* Stephens, 1834	*Pinus mugo*, *Pinus nigra*, *Pinus sylvestris*, *Pinus uncinata*	Europe
Yponomeutidae	*Ocnerostoma friesei* Svensson, 1966	*Pinus mugo*, *Pinus sylvestris*	Europe
Yponomeutidae	*Ocnerostoma piniariella* Zeller, 1847	*Pinus cembra*, *Pinus contorta* var. *latifolia*, *Pinus monticola*, *Pinus mugo*, *Pinus resinosa*, *Pinus strobus*, *Pinus sylvestris*	North America*, Europe
Yponomeutidae	*Ocnerostoma* sp.	*Pinus resinosa*	North America
Yponomeutidae	*Ocnerostoma strobivorum* Freeman, 1960	*Pinus strobus*	North America
Yponomeutidae	*Zelleria haimbachi* Busck, 1915	*Pinus arizonica*, *Pinus attenuata*, *Pinus banksiana*, *Pinus contorta*, *Pinus coulteri*, *Pinus echinata*, *Pinus engelmannii*, *Pinus jeffreyi*, *Pinus muricata*, *Pinus ponderosa*, *Pinus radiata*, *Pinus resinosa*, *Pinus sylvestris*, *Pinus taeda*	North America
Diptera			
Agromyzidae	*Liriomyza schmidti* Aldrich, 1929	?*Zamia integrifolia*	North America
Coleoptera			
Curculionidae	*Brachonyx pineti* Paykull, 1792	*Pinus sylvestris*, *Pinus uncinata*	Europe

Note: Detailed information such as insect taxonomy, host taxonomy and local distribution are provided in Suppl. materials 1, 2. An asterisk marking the name

of a continent (e.g. Europe*) indicates that the corresponding herbivore species is introduced in that region. A question mark "?" before an insect name indicates that this species has not been confirmed as a leafminer and a question mark "?" before a plant name indicates that its status as a host of the corresponding insect species requires confirmation.

Table 2.

Number of gymnosperm-feeding leafminer species and number of host plant species used by these insects, in different leafminer families in North America (NA) and Europe (EU).

Leafminer order	Leafminer family	Number of leafminer species in each leafminer family	Number of host species in each leafminer family	Leafminer genus	Number of leafminer species in each leafminer genus	Number of host species in each leafminer genus
Lepidoptera	Tortricidae	53 (NA: 43, EU: 12)	64 (NA: 58, EU: 13)	*Rhyacionia*	19 (NA: 19, EU: 0)	21 (NA: 21, EU: 0)
				Epinotia	13 (NA: 8, EU: 6)	19 (NA: 15, EU: 6)
				Choristoneura	9 (NA: 9, EU: 0)	22 (NA: 22, EU: 0)
				Argyrotaenia	3 (NA: 3, EU: 0)	14 (NA: 14, EU: 0)
				Archips	2 (NA: 1, EU: 1)	20 (NA: 15, EU: 6)
				Taniva	1 (NA: 1, EU: 0)	7 (NA: 7, EU: 0)
				Spilonota	1 (NA: 1, EU: 1)	4 (NA: 2, EU: 3)
				Pseudohermenias	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)
				Dichelia	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)
				Cymolomia	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)
				Clavigesta	1 (NA: 0, EU: 1)	3 (NA: 0, EU: 3)
				Aethes	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)
	Gelechiidae	42 (NA: 41, EU: 4)	50 (NA: 45, EU: 10)	*Coleotechnites*	33 (NA: 33, EU: 1)	31 (NA: 30, EU: 2)

				Exoteleia	6 (NA: 6, EU: 1)	20 (NA: 18, EU: 4)
				Chionodes	2 (NA: 1, EU: 1)	7 (NA: 3, EU: 4)
				Dichomeris	1 (NA: 1, EU: 1)	2 (NA: 1, EU: 1)
	Argyresthiidae	20 (NA: 14, EU: 8)	28 (NA: 13, EU: 22)	*Argyresthia*	20 (NA: 14, EU: 8)	28 (NA: 13, EU: 22)
	Yponomeutidae	7 (NA: 4, EU: 4)	22 (NA: 17, EU: 7)	*Ocnerostoma*	4 (NA: 3, EU: 2)	7 (NA: 4, EU: 3)
				Cedestis	2 (NA: 0, EU: 2)	6 (NA: 0, EU: 6)
				Zelleria	1 (NA: 1, EU: 0)	14 (NA: 14, EU: 0)
	Batrachedridae	2 (NA: 1, EU: 2)	7 (NA: 4, EU: 4)	*Batrachedra*	2 (NA: 1, EU: 2)	7 (NA: 4, EU: 4)
	Pyralidae	2 (NA: 2, EU: 0)	22 (NA: 22, EU: 0)	*Dioryctria*	1 (NA: 1, EU: 0)	11 (NA: 11, EU: 0)
				Pococera	1 (NA: 1, EU: 0)	11 (NA: 11, EU: 0)
	Coleophoridae	1 (NA: 1, EU: 1)	7 (NA: 6, EU: 7)	*Coleophora*	1 (NA: 1, EU: 1)	7 (NA: 6, EU: 7)
	Noctuidae	1 (NA: 1, EU: 0)	13 (NA: 13, EU: 0)	*Feralia*	1 (NA: 1, EU: 0)	13 (NA: 13, EU: 0)
	Blastobasidae	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)	*Blastobasis*	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)
	Adelidae	1 (NA: 0, EU: 1)	1 (NA: 0, EU: 1)	*Nemophora*	1 (NA: 0, EU: 1)	1 (NA: 0, EU: 1)
	Bucculatricidae	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)	*Bucculatrix*	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)
Diptera	Agromyzidae	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)	*Liriomyza*	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)

Coleoptera	Curculionidae	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)	*Brachonyx*	1 (NA: 0, EU: 1)	2 (NA: 0, EU: 2)

Table 3.

Number of host species and associated leafminer species in different gymnosperm plant families in North America (NA) and Europe (EU).

Gymnosperm family	**Number of host species in each gymnosperm family**	**Number of leafminers in each gymnosperm family**	**Gymnosperm genus**	**Number of host species in each gymnosperm genus**	**Number of leafminers in each gymnosperm genus**
Pinaceae	74 (NA: 65, EU: 29)	102 (NA: 83, EU: 26)	*Pinus*	38 (NA: 35, EU: 8)	67 (NA: 59, EU: 10)
			Abies	12 (NA: 7, EU:9)	31 (NA: 18, EU:13)
			Picea	10 (NA: 9, EU: 5)	28 (NA: 18, EU: 13)
			Larix	8 (NA: 8, EU: 6)	10 (NA: 8, EU: 4)
			Tsuga	4 (NA: 4, EU: 0)	9 (NA: 9, EU: 0)
			Pseudotsuga	2 (NA: 2, EU: 1)	7 (NA: 6, EU: 1)
Cupressaceae	26 (NA: 18, EU: 16)	32 (NA: 25, EU: 10)	*Juniperus*	14 (NA: 9, EU: 9)	22 (NA: 15, EU: 9)
			Cupressus	3 (NA: 1, EU: 2)	6 (NA: 4, EU: 3)
			Thuja	3 (NA: 2, EU: 3)	7 (NA: 5, EU: 4)
			Chamaecyparis	2 (NA: 2, EU: 2)	5 (NA: 2, EU: 4)
			Calocedrus	1 (NA: 1, EU: 0)	2 (NA: 2, EU: 0)
			Sequoia	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)
			Taxodium	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)
			Platycladus	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)
Taxaceae	1 (NA: 0, EU: 1)	1 (NA: 0, EU: 1)	*Taxus*	1 (NA: 0, EU: 1)	1 (NA: 0, EU: 1)
Zamiaceae	1 (NA: 1, EU: 0)	1 (NA: 1, EU: 0)	*Zamia*	1 (NA: 1, EU:0)	1 (NA: 1, EU: 0)

Supplementary materials

Suppl. material 1: The gymnosperm-feeding leafminers and their host plants in North America

Authors: Taibin Chen, Xiaohua Dai, Charles Eiseman
Data type: Number of species
Download file (33.35 kb)

Suppl. material 2: The gymnosperm-feeding leafminers and their host plants in Europe

Authors: Taibin Chen, Xiaohua Dai, Charles Eiseman
Data type: Number of species
Download file (19.06 kb)

Suppl. material 3: Insect families of leafminers on ferns, gymnosperms, angiosperms in North America and Europe

Authors: Taibin Chen, Xiaohua Dai, Charles Eiseman
Data type: Insect families
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