

## The insect community of *Plantago lanceolata* spikes in the Åland Islands, SW Finland

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We describe the structure of the insect community of *Plantago lanceolata* spikes based on rearings collected from Åland Islands and literature. Our main focus was on occurrences and local abundances of the host-specific *Mecinus pascuorum* (Coleoptera: Curculionidae), its main parasitoid *Mesopolobus incultus* (Hymenoptera: Pteromalidae) and two hyperparasitoids *Baryscapus endemus* (Hymenoptera: Eulophidae) and *Eupelmus vesicularis* (Hymenoptera: Eupelmidae). Sampling was performed in two networks of habitat patches in 2000 and 2001 (89 patches), and in 18 networks in 2009 (643 patches). We detected five herbivorous, one predatory and 33 parasitoid taxa of Coleoptera, Diptera and Hymenoptera, as well as several Hemiptera and Thysanoptera species. *Clinodiplosis cilicrus* (Kieffer, 1889) (Diptera: Cecidomyiidae) is reported as new to Finland. All four focal species were very abundant. The rest of the species occurred rather sporadically and were mainly generalists either feeding on *P. lanceolata* spikes or attacking insects feeding on spikes or their parasitoids.

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### 1. Introduction

A broad definition of community ecology is the study of patterns and processes involving at least two species at a particular location (Morin 2011). The patterns that community ecology aims to explain typically include diversity, species richness, productivity and food-web organization on various spatial and temporal scales (e.g. Morin 2011, Rossberg 2013). The focus may be widened from community structure to the metacommunity level, i.e. to the study on the spatiotemporal dynamics among local communities that consist of a

group of species potentially occupying patches of the same habitat type within a certain region (Holyoak *et al.* 2005).

One of the best-known metacommunities includes the Glanville fritillary butterfly (*Melitaea cinxia* [Linnaeus]), its host plants, and its specialist larval parasitoid and hyperparasitoid wasps in the Åland Islands located in the SW archipelago of Finland (e.g. Lei *et al.* 1997, van Nouhuys & Hanski 2005). The spatiotemporal dynamics of these species have been studied for two decades, and the dynamic equilibrium of extinctions and colonisations has been plausibly demonstrated

(e.g. Hanski 1999, van Nouhuys & Hanski 2002, Ojanen *et al.* 2013). While variation in host plant quality and a range of abiotic factors are known to affect the life stages of *M. cinxia*, the possible effects of and interactions with other species consuming the same host plants remain largely unknown (Nieminen *et al.* 2004). However, there is one noteworthy exception: effects of the mildew fungus *Podosphaera plantaginis* (Castagne) U. Braun & S. Takamatsu infecting leaves of the ribwort plantain (*Plantago lanceolata* L.) on *M. cinxia* larvae and its specialist parasitoids have been thoroughly studied (Laine 2004, van Nouhuys & Laine 2008).

The insect community associated with *P. lanceolata* in Åland includes several specialist and generalist herbivores (other than *M. cinxia*), as well as their parasitoids and hyperparasitoids. Our knowledge of these species has been limited to the literature and sporadic observations from the field. Here we present detailed studies on the identity and natural history of species using the spikes (or seed-heads) of *P. lanceolata*. The main focus is on the monophagous weevil *Mecinus pascuorum* (Gyllenhal) (Coleoptera: Curculionidae), which is a predispersal seed predator (granivore), and its parasitoid wasps (see Vikberg & Nieminen 2012). This information will subsequently be used to study their (meta)population biology, and to allow for comparisons of metacommunity dynamics between the spike-inhabiting insect community and the co-occurring food-web compartment associated with the leaf-feeding *M. cinxia*.

As a monophagous seed predator of *P. lanceolata*, *M. pascuorum* may be considered a key species in the population dynamics of its host plant for at least two reasons. First, seed predators often inflict high seed mortality causing variability, even strong declines, in population sizes of a host plant and, simultaneously, also affecting other herbivores sharing the same host (e.g. Andersen 1988, Crawley 2000). *Plantago lanceolata* is a perennial herb, which reproduces both vegetatively and by seed (Latzel *et al.* 2009). It occasionally suffers high mortality due to severe regional droughts (Hanski & Meyke 2005, own observations by MN). While vegetative reproduction may play a strong role in normal years, re-growth of *P. lanceolata* populations af-

ter such population crashes may be significantly slowed down, if *M. pascuorum* has reduced the seed bank. Second, the dispersal rate of seeds is diminished due to seed predation. This affects the spatial distribution of seeds and seed bank within habitat patches, and reduces (re)colonization rate of empty habitat patches. Reduced seed production can also reduce gene flow among populations (e.g. Crawley 2000, Cousens *et al.* 2008), though pollen dispersal also makes an important contribution to gene flow (Rubio de Casas *et al.* 2012).

A couple of population ecological studies of *M. pascuorum* have previously been performed. Effects of spatial scale of habitat occurrence on interactions between *P. lanceolata*, *M. pascuorum* and its primary parasitoid wasp *Mesopolobus incultus* (Walker) were studied in two sites in southern England (Mohd Norowi *et al.* 1999, 2000). They found that the density of available spikes varied among years with a direct effect on weevil abundance which in turn directly affected parasitoid densities. Spatial scale had no significant effect on spike and weevil densities, but variability in parasitoid densities increased and the type of density-dependence changed with increasing spatial scale. Hancock *et al.* (2013), Herbst *et al.* (2013) and Wäschke *et al.* (2014) have studied the same three species in Germany (three regions and years, totally 76–80 sites). They have found that besides spike density, also land use intensity and type, plant diversity, and, consequently, primary and secondary metabolite content of host plants may influence population dynamics of *M. pascuorum* and its natural enemies.

Here, we describe the structure of the insect community of the *P. lanceolata* spikes in the Åland Islands. This community includes specialist and generalist herbivores, parasitoids, hyperparasitoids and predators. We also describe the interspecific interactions based on laboratory rearings and literature. This study forms the basis for detailed food-web and metacommunity studies, which will be presented elsewhere.

## 2. Material and methods

*Mecinus pascuorum* is a monophagous seed predator of *P. lanceolata*. Females use odours to lo-

Table 1. Numbers of Coleoptera, Diptera and Hymenoptera individuals that emerged from rearings in 2000 and 2001. Numbers of occupied patches are given in parentheses for the most abundant species.

Species	Föglö 2000	Föglö 2001	Jomala 2000	Jomala 2001
<b>Coleoptera</b>				
Chrysomelidae				
<i>Longitarsus pratensis</i>	1			
Curculionidae				
<i>Mecinus pascuorum</i>	55 (28)	192 (31)	49 (22)	67 (24)
<i>Trichosirocalus troglodytes</i>	1			
Total Coleoptera spp.	3	1	1	1
Total Coleoptera inds.	57	192	49	67
<b>Diptera</b>				
Agromyzidae				
<i>Phytomyza plantaginis</i>	3	10		2
<b>Hymenoptera</b>				
Platygastroidea				
Scelionidae: Telenominae				
<i>Telenomus</i> sp.	1	6		
Cynipoidea				
Figitidae: Charipinae				
<i>Alloxysta</i> sp.		1		
Chalcidoidea				
Eulophidae: Entedoninae				
<i>Chrysocharis pubicornis</i>		7		2
<i>Neochrysocharis formosa</i>		3		
<i>Pediobius metallicus</i>	1	1		
Eulophidae: Tetrastichinae				
<i>Aprostocetus</i> sp.			1	
<i>Baryscapus endemus</i>	1	25		2
Eupelmidae: Eupelminae				
<i>Eupelmus vesicularis</i>	10 (6)	56 (13)	5 (3)	23 (11)
Pteromalidae: Miscogastrinae				
<i>Thinodytes cyzicus</i>		2		
Pteromalidae: Pteromalinae				
<i>Mesopolobus incultus</i>	231 (24)	582 (31)	134 (17)	211 (22)
<i>Pteromalus</i> sp.	2	15		
<i>Pteromalus semotus</i>		5		
Ichneumonoidea				
Ichneumonidae: Cryptinae				
<i>Dichrogaster aestivalis</i>	1	1		
Braconidae: Aphidiinae				
<i>Aphidius</i> sp.		1		
<i>Trioxys</i> sp.			1	
Braconidae: Braconinae				
<i>Bracon delibator</i>	3	2	1	
Braconidae: Opiinae				
Opiinae sp.		7		
<i>Opius pallipes</i>		1		
<i>Phaedrotoma depeculator</i>		1		
<i>Phaedrotoma diversa</i>		1		
Total Hymenoptera spp.*	7	17	5	4
Total Hymenoptera inds.	249	718	142	238

Notes. Nomenclature follows Silfverberg 2010 (Coleoptera), Spencer 1976 (Diptera) and Dathe *et al.* 2001 (Hymenoptera). Patch networks included: 37: Föglö, Överö/Ulversö (46 patches; samplings on 3.VIII.2000 and 1.VIII.2001), 57: Jomala, Öningeby/Västerkalmare (43 patches; samplings on 1.VIII.2000 and 30.–31.VII.2001).

\* Opiinae sp. is not counted.

Table 2. Numbers of Coleoptera, Diptera and Hymenoptera individuals that emerged from rearings in 2009. Numbers of occupied patches are shown for the four most abundant species.

	Habitat patch network ID									
	2	9	11	27	36	37	40	47	50	57
No. of patches	20	43	64	8	53	30	70	33	109	57
<b>Coleoptera</b>										
Curculionidae										
<i>Mecinus pascuorum</i>	109	6	124	13	121	266	3	26	8	275
Occupied patches*	14	2	40	4	29	26	4	13	6	38
<b>Diptera</b>										
Cecidomyiidae										
<i>Clinodiplosis cilicrus</i>	1		1		1				1	
<i>Lestodiplosis</i> sp.			5		2	4			2	2
Agromyzidae										
<i>Phytomyza plantaginis</i>			1			1			2	2
Total Diptera spp.	1	0	3	0	2	2	0	0	3	2
<b>Hymenoptera</b>										
Platygastridae										
Scelionidae: Telenominae										
<i>Telenomus chloropus</i>							2		1	
<i>Telenomus</i> sp.1							1		4	
<i>Telenomus</i> sp.2									3	1
<i>Telenomus</i> sp.3?	1									
<i>Trissolcus grandis</i>							14			2
<i>Trissolcus</i> sp.										
Chalcidoidea										
Eulophidae: Entedoninae										
<i>Chrysocharis pubicornis</i>			1							
<i>Neochrysocharis formosa</i>							1			
<i>Pediobius metallicus</i>					1		1		2	
Eulophidae: Tetrastichinae										
<i>Aprostocetus</i> sp.1										1
<i>Aprostocetus</i> sp.2										1
<i>Aprostocetus</i> sp.3										1
<i>Baryscapus endemus</i>	4	3	18	1	21	142	1	4	1	59
Occupied patches	2	1	4	1	9	19	1	1	1	20
Eupelmidae: Eupelminae										
<i>Eupelmus vesicularis</i>	121	1	156	5	181	446	4	37	5	103
Occupied patches	13	1	18	2	22	26	3	6	4	21
Mymaridae										
<i>Polynema</i> sp.							2			
Pteromalidae: Pteromalinae										
<i>Mesopolobus incultus</i>	189	13	402	55	357	784	22	73	29	688
Occupied patches	13	2	33	3	24	24	3	11	6	32
<i>Mesopolobus</i> sp.						2				1
<i>Pteromalus semotus</i>						3				2
<i>Pteromalus</i> sp.1	1					2				
<i>Pteromalus</i> sp.2	1				1	5		1		1
<i>Pteromalus</i> sp.3							1			2
<i>Pteromalus</i> sp.4									1	
Ichneumonidae										
Ichneumonidae: Cryptinae										
<i>Dichrogaster aestivalis</i>									1	
<i>Gelis</i> sp.										
Braconidae: Aphidiinae										
<i>Aphidius</i> sp.									1	
<i>Ephedrus</i> sp.										1
Braconidae: Braconinae										
<i>Bracon delibator</i>					1	2	1	2		
Braconidae: Opiinae										
<i>Phaedrotoma depeculator</i>							1			
Ceraphronoidea: Ceraphronidae										
<i>Aphanogmus</i> sp.										
<i>Ceraphron</i> sp.										
Total Hymenoptera spp.	6	3	4	3	5	8	12	5	10	12

Table 2. Continued.

	Habitat patch network ID								
	63	75	106	108	111	116	117	123	Total
No. of patches	14	34	11	14	23	32	17	11	643
<b>Coleoptera</b>									
Curculionidae									
<i>Mecinus pascuorum</i>			158	1	86	21		3	1,220
Occupied patches*	0	2	9	1	17	12	1	1	219
<b>Diptera</b>									
Cecidomyiidae									
<i>Clinodiplosis cilicrus</i>	1								5
<i>Lestodiplosis</i> sp.									15
Agromyzidae									
<i>Phytomyza plantaginis</i>									6
Total Diptera spp.	1	0	0	0	0	0	0	0	3
<b>Hymenoptera</b>									
Platygastridae									
Scelionidae: Telenominae									
<i>Telenomus chloropus</i>									12
<i>Telenomus</i> sp.1					7				4
<i>Telenomus</i> sp.2									1
<i>Telenomus</i> sp.3?									16
<i>Trissolcus grandis</i>									1
<i>Trissolcus</i> sp.	1								1
Chalcidoidea									
Eulophidae: Entedoninae									
<i>Chrysocharis pubicornis</i>								1	1
<i>Neochrysocharis formosa</i>								1	5
<i>Pediobius metallicus</i>					1				1
Eulophidae: Tetrastichinae									
<i>Aprostocetus</i> sp.1					1				24
<i>Aprostocetus</i> sp.2			2		21				1
<i>Aprostocetus</i> sp.3									19
<i>Baryscapus endemus</i>			19		50	23		3	349
Occupied patches	0	0	3	0	10	6	0	1	79
Eupelmidae: Eupelminae									
<i>Eupelmus vesicularis</i>		1	164		92	29		4	1,349
Occupied patches	0	1	7	0	12	4	0	1	141
Mymaridae									
<i>Polynema</i> sp.									2
Pteromalidae: Pteromalinae									
<i>Mesopolobus incultus</i>		11	237		302	64	1	25	3,252
Occupied patches	0	2	9	0	16	11	1	1	191
<i>Mesopolobus</i> sp.			1		1				5
<i>Pteromalus semotus</i>									5
<i>Pteromalus</i> sp.1			3						6
<i>Pteromalus</i> sp.2		1							10
<i>Pteromalus</i> sp.3									3
<i>Pteromalus</i> sp.4									1
Ichneumonidae									
Ichneumonidae: Cryptinae									
<i>Dichrogaster aestivalis</i>								1	2
<i>Gelis</i> sp.				1					1
Braconidae: Aphidiinae									
<i>Aphidius</i> sp.									1
<i>Ephedrus</i> sp.									1
Braconidae: Braconinae									
<i>Bracon delibator</i>			1	1				1	9
Braconidae: Opiinae									
<i>Phaedrotoma depeculator</i>								1	
Ceraphronoidea: Ceraphronidae									
<i>Aphanogmus</i> sp.						1			1
<i>Ceraphron</i> sp.						1			1
Total Hymenoptera spp.	1	3	7	2	8	5	1	5	30

Notes. Nomenclature follows Silfverberg 2010 (Coleoptera), Spencer 1976 (Diptera) and Dathe *et al.* 2001 (Hymenoptera).

Locations of habitat patch networks (sampling dates in parentheses): 2: Föglö, Hummersö/Kallsö (4.VIII), 9: Eckerö, Böle/Kyrkoby (30.VII), 11: Lemland, Flaka/Vessingsboda (2.VIII), 27: Hammarland, Bondtorp/Östanträsk (1.VIII), 36: Lumparland, Svinö (7.–8.VIII), 37: Föglö, Överö (4.VIII), 40: Hammarland, Äspholm/Skarpnätö/Strömma (31.VII), 47: Jomala, Brändö/Gottby/Kungsö (2.–3.VIII), 50: Sund, Bomarsund/Finby (2. & 5.VIII), 57: Jomala, Önningeby/Österkalmare/Västerkalmare (29.–31.VII), 63: Hammarland, Samuelstorp/Torp (1.VIII), 75: Vårdö, Östra Simskäla (6.VIII), 106: Föglö, Flisö/Kallsö (4.VIII), 108: Vårdö, Bussö (7.VIII), 111: Lemland, Järsö/Skedholm (8.VIII), 116: Finström, Rågetsböle/Torrbolstad (1.VIII), 117: Sund, Hulta (1.VIII), 123: Geta, Dånö (8.VIII).

\* Includes also patches from where only parasitoids of *M. pascuorum* emerged.

cate host plants (Wäschke *et al.* 2014). They lay one egg per developing seed capsule, and each larva consumes the contents of a capsule (usually two seeds; Dickason 1968, Mohd Norowi *et al.* 1999). Pupation takes place within the seed capsule (Scherf 1964, Dickason 1968, own observations). In Åland, adult emergence starts in July peaking around early August and continues until early September, at least (own observations by MN). It overwinters in the adult stage. In spring, adults break the diapause in April and are most active in late May and June. The latest adult individuals have been seen on the flower heads around mid-July (own observations by MN).

Occurrences and local abundances of *M. pascuorum* and its main parasitoid wasp *Mesopolobus incultus* (Walker) (Hymenoptera: Pteromalidae) were studied in Åland over three years. Sampling was performed in two networks of habitat patches in 2000 and 2001 (Föglö Ulversö/Överö and Jomala Önningsby, totally 89 patches; Table 1). In 2009, 18 networks and a total of 643 *P. lanceolata* patches (size range some 0.002–5.5 ha) were included (Table 2). All patches within each network were sampled from late July to early August (see Tables 1 & 2). Habitat patches are continuous, mostly open meadows and pastures with *P. lanceolata*, while patch networks are groups of habitat patches that are dynamically highly independent of each other (i.e. only occasional dispersal of individuals among networks; see Nieminen *et al.* 2004 and Ojanen *et al.* 2013 for a more thorough description of the study area). However, patches and networks have been defined based on the population biology of *M. cinxia*, and we have adopted these definitions here. In addition to these systematic samplings, sporadic samples of insects encountered on *P. lanceolata* spikes are included in order to include all information we have. Because this study aimed at compiling reliable data on the two focal species, phenologically earlier (and later) species were partly or completely missed, if such species occur in Åland. To gather more complete data of the whole community sampling should be repeated at different times of the season. Because of the timing of our sampling, the earliest individuals of *M. pascuorum* and its parasitoids and hyperparasitoids (*M. incultus*, *E. vesicularis* [Retzius] & *B. endemus* [Walker]) were also

missed. However, this occurred in about the same proportion in different habitat patch networks. Even with this bias, it is highly unlikely that we would have missed populations of *M. pascuorum* or its parasitoid due to phenological differences, because their emergence periods last more than a month.

The number of spikes sampled per patch depended on the total abundance of *P. lanceolata* in the patch. In 2000 and 2001, we collected 20, 15 or 10 spikes in patches where *P. lanceolata* was very abundant, moderately abundant or sparse, respectively. In 2009, spikes were sampled from different parts of each patch, and each spike originated from a different plant individual. As the whole habitat patch was covered in the sampling, the number of spikes collected depended on the coverage of *P. lanceolata*. However, when the number of spikes was very low maximally some 10% of spikes were collected. This procedure resulted in collection of 1–161 spikes per patch (30.7 spikes on average). All spikes from each patch were collected into a plastic bag coded with the patch identification number. A piece of paper towel was included to inhibit condensing moisture. Stalks were cut with scissors several centimetres below the spike. The aim was to only collect spikes with ripe seeds, but if they were not available younger or older (a part of seeds already fallen off) spikes were sampled. Also, spikes of *Plantago major* L. and *P. media* L. were collected where they were abundant on the same patches, but no *M. pascuorum* and altogether very few insects emerged from them.

Bags were kept indoors in a shaded place until the end of sampling, and then spikes were transferred singly into coded transparent plastic tubes with a small piece of paper towel at the bottom. Every year some weevils and wasps emerged while still in the plastic bags. In 2009, spikes from such bags were placed in larger transparent plastic cups with a gauze top (i.e. not singly). All individuals originating from bags with emerged weevils or wasps were coded with the patch number only, whereas all insects that emerged in the tubes were additionally coded with an individual spike code. Seeds that dropped off in bags were placed in a separate tube. In 2000 and 2001, the tubes were closed with caps and papers were replaced a couple of times during the first two weeks of rear-

ing. If mould started to grow, the tubes were kept open for a couple of days. In 2009, the tubes were capped with gauze if mould appeared. The tubes were checked daily until no mould appeared on any spike, and then again after about a month when emerged individuals were transferred into coded eppendorf tubes (Cecidomyiidae flies were not kept in 2000 and 2001). Most insects were later glued on mounting cards for identification. Samples were not retained over winter.

Identifications based on morphology were performed by experts: Coleoptera by Olof Biström, Ilpo Mannerkoski, Jyrki Muona and MN, Diptera by Jere Kahanpää (Agromyzidae) and Marcela Skuhrová (Cecidomyiidae), Hemiptera by Anders Albrecht, Hymenoptera by VV, and Thysanoptera by Jukka Kettunen.

### 3. Results

The species complex associated with *P. lanceolata* spikes includes highly specialized to widely generalist species (Fig. 1; details on the biology of all Coleoptera, Diptera, Hemiptera, Hymenoptera and Thysanoptera taxa encountered are presented in Appendix A). Abundances of all five herbivorous, one predatory and 33 parasitoid taxa of Coleoptera, Diptera and Hymenoptera recorded from the rearings are listed in Tables 1 and 2. Various herbivorous taxa and their natural enemies form largely separate food-web compartments or modules (Fig. 1). Four species forming one compartment (*M. pascuorum*, *M. incultus*, *Eupelmus vesicularis* [Retzius] & *Baryscapus endemus* [Walker]) were very abundant, while the rest of the species were much rarer (Tables 1 & 2).

Among patch networks, the highest number of parasitoid species detected was 17 in Föglö Överö in 2001 (46 patches; average patch number among networks in all years = 36.4). Remarkably, the numbers of parasitoid species in that same network was in 2000 and 2009 only seven and eight species, respectively, which are very close to the average of six species among networks in all years.

The numbers of parasitoid individuals varied a lot among networks and years. For example, there were 249, 718 and 1,386 individuals in

Föglö Överö in 2000, 2001 and 2009, respectively. Hence, the number of individuals did not explain the number of species in a particular network. Nevertheless, the lower number of patches sampled in Föglö Överö in 2009 may have had a negative effect on the number of species detected.

Overall, there was considerable variation among the patch networks in the numbers of species and individuals of all taxa in 2009 (Table 2). This variability and reasons for it, as well as rates of parasitism, will be studied in detail elsewhere.

### 4. Discussion

The insect community of *P. lanceolata* spikes is surprisingly diverse in Åland (Fig. 1). However, the community mainly consists of generalist species, as only the two weevil species (*M. pascuorum* and *Trichosirocalus troglodytes* [Fabricius]) are specialists, the latter of which was only occasionally found in the spikes (see Appendix A). In addition, the agromyzid fly *Phytomyza plantaginis* Robineau-Desvoidy is oligophagous on *Plantago* spp. Several other *P. lanceolata* specialist herbivores (and most probably also generalists) are known to occur in Baltic countries and/or Sweden, for example the weevil *Mecinus pyraeter* (Herbst) and the cecidomyiid *Jaapiella schmidtii* (Rübsaamen) (Silfverberg 2010, Bisby *et al.* 2011).

The food-web associated with *P. lanceolata* spikes has a high level of compartmentalization with apparently little interactions between compartments but strong interactions within them. There are four very abundant species in the main food-web compartment including *M. pascuorum* and its parasitoids and hyperparasitoids (*M. incultus*, *E. vesicularis* & *B. endemus*; Fig. 1, Tables 1 & 2, Appendix A). More detailed studies are needed to reveal specific aspects of the interactions among these species. For example, there may be temporal variability in the parasitism rate of *M. pascuorum* larvae, or some weevil larvae may even escape parasitism completely, because the weevil's egg-laying period is long and parasitoid occurrence may not cover it entirely. Such temporal variability in parasitism rate could have significant population dynamical consequences for *M. pascuorum*. Additionally, the ex-

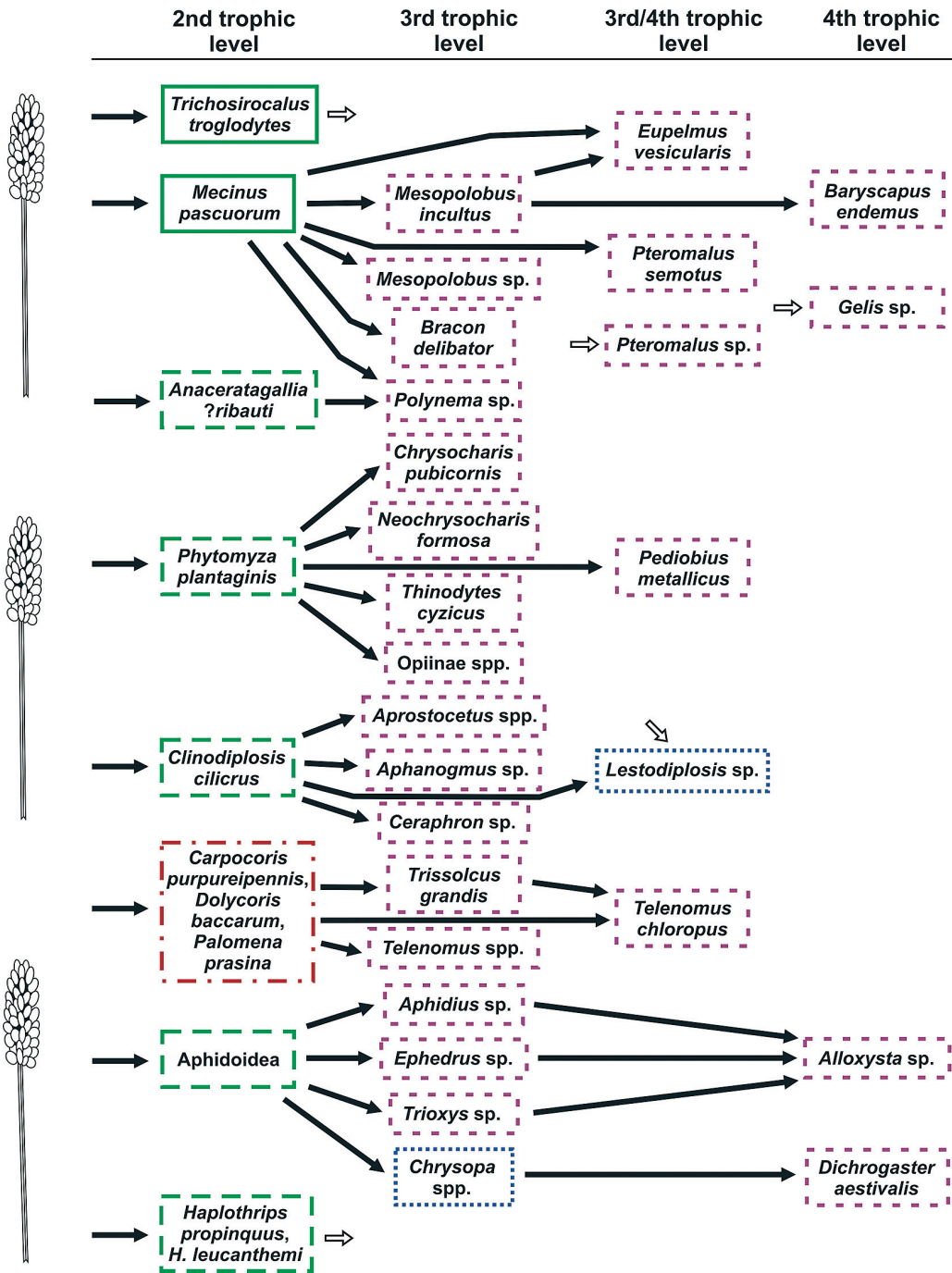


Fig. 1. Connectance food-web of all insect species recorded from the spikes of *P. lanceolata* in Åland. Aphidoidea species did not occur in these samples, but they are relatively common (Nieminen *et al.* 2004). Arrows: black = known or inferred interspecific interactions (herbivory, parasitism and predation [competitive or mutualistic interactions are unknown]) based on the literature (see Appendix A) or/and observed in this study, white = interactions that exist but remained unknown in this study. Boxes: continuous line = specialist herbivore, long-dash line = oligo/polyphagous herbivore, short-dash line = oligo/polyphagous parasitoid, dotted line = predator, dot-dash line = omnivore.



act role of *E. vesicularis* is currently uncertain, but potentially crucial for the population dynamics of all four species. According to the literature (see Appendix A), it is likely an omnivorous species parasitizing both *M. pascuorum* and *M. incultus*. But it remains unknown whether this really is the case in this community, and if so, whether *E. vesicularis* prefers one over the other.

The spatial population dynamics of *M. pascuorum* and *M. pyraeaster* and their primary parasitoids have been studied in Great Britain by Mohd Norowi *et al.* (1999, 2000), and *M. pascuorum* and *Mecinus labilis* (Herbst) and their primary parasitoids in Germany by Hancock *et al.* (2013) and Herbst *et al.* (2013). In those studies, *M. incultus* was the only abundant parasitoid (the rare parasitoids emerging from their rearings were not named) attacking *M. pascuorum* with parasitism rates 0.11–0.45 for three site-year combinations in the British study (not reported in German studies; total parasitism rates were 0.73–1 in Åland [M. Nieminen, unpubl.]). This may reflect a notable difference between the British and German study sites and Åland, because both *E. vesicularis* and *B. endemus* were present (and often abundant) only in Åland, and in most habitat patch networks there (Tables 1 & 2). On the other hand, the spatial extent of study sites of Mohd Norowi *et al.* (1999, 2000) corresponds better to habitat patches not patch networks. Because *E. vesicularis* was absent from quite many patches in Åland, its absence in the British study may result from chance only. This does not, however, explain the results from Germany, where in total 76–80 habitat patches within three geographical regions were sampled in three years. Here the difference may simply result from the considerably later sampling period in Germany than in Åland leading to possible mismatch with the phenology of *E. vesicularis*.

The other, mainly generalist, species we collected occurred more or less sporadically in the sampled spikes (Tables 1 & 2). All species encountered appear to actually be associated with the spike food-web, because they may either feed on *P. lanceolata* spikes or attack insects feeding on spikes or their parasitoids (see Appendix A for details).

Spikes of *P. lanceolata* also harbor quite a few species other than insects, for example the fungus

*Phomopsis subordinaria* (Desm.) Trav. which usually kills the infected spike (de Nooij & van der Aa 1987, Laine 2003). If considering the entire plant the number of interacting species increases even more remarkably. Furthermore, *P. lanceolata* itself, as well as all species consuming it and their consumers are hosts to an unknown number of generalist herbivores (e.g. grasshoppers, root-herbivores and domestic animals; Lacey *et al.* 2003, Hanley 2012, Sonnemann *et al.* 2012), predators (e.g. spiders, various insects and birds; Nieminen *et al.* 2004), parasites (e.g. nematodes and fungi, hemiparasitic vascular plants; Cameron *et al.* 2008, Wurst *et al.* 2009), pathogens (fungi, bacteria and viruses; Gonda *et al.* 2013), mutualists (e.g. gut bacteria and protists, mycorrhizae; Gange & West 1994, Ayres *et al.* 2006, Lachowska *et al.* 2010, Larimer *et al.* 2010) and decomposers (e.g. Ladygina *et al.* 2010, Eisenhauer & Reich 2012) with variable competitive, antagonistic and potentially synergistic interactions (e.g. Haase *et al.* 2008, Bezemer *et al.* 2010, Vázquez-de-Aldana *et al.* 2011, Verlinden *et al.* 2013). For the weevil *M. pascuorum*, the only interaction known (besides the host plant and parasitoids) is with endosymbiotic *Wolbachia* bacteria that inhabit most individuals sampled in Åland (Anne Duplouy, pers. comm.), and are common among weevils (Lachowska *et al.* 2010). Taken together, the food-web associated with *P. lanceolata* is highly complex including probably even several hundred species in total. As this complexity is also linked with various environmental factors, the spatio-temporal dynamics of such systems are currently not possible to study empirically or even theoretically (e.g. Harrison *et al.* 2005). On the other hand, the dynamics of compartmentalized subsystems, like *M. pascuorum* and its parasitoid complex, can be adequately understood without a comprehensive knowledge of (all) other subsystems.

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## Appendices

### Appendix A. Biology of species.

The biology of all taxa encountered on or emerged from rearings of spikes of *Plantago lanceolata* in Åland is briefly described (for species which do not depend on the spikes for their development, only some basic information is presented). Species that we have interpreted as being closely associated with *P. lanceolata* spikes (herbivores and their parasitoids and hyperparasitoids) are indicated by a star (\*) before the name. All individuals were reared from *P. lanceolata* spikes, unless otherwise noted. For species-level identifications, all observations are listed. Coordinates are presented in the Finnish National Coordinate System (yhtenäiskoordinaatisto, YKJ) with 1 km<sup>2</sup> accuracy. The dates indicate the day(s) when rearings were taken from the field. All samples were collected by MN, except in the year 2009 by Metapopulation Research Group. For a detailed description of the biology of *P. lanceolata* see Sagar and Harper (1964), Cavers *et al.* (1980) and Kuiper and Bos (1992).

### A1. Coleoptera

Chrysomelidae: Alticinae

*Longitarsus pratensis* (Panzer, 1794)

An oligophagous species that feeds on leaves leaving roundish holes on *Plantago* species, especially *P. lanceolata*, as an adult; larvae feed on the mesophyll (Kevan 1967, Döberl 1994, Crémieux *et al.* 2008, Anonymous 2013). It overwinters as an adult in moss, possibly also as eggs and larvae (Anonymous 2013). It is a wing-polymorphic species, and the majority of individuals had reduced wings in Great Britain (Shute 1980).

Observation: Föglö, Överö (6683:3139) 1 ind. 3.VIII.2000.

Curculionidae

Curculioninae

\**Mecinus (Gymnetron) pascuorum* (Gyllenhal, 1813)

A monophagous seed predator of *P. lanceolata* (see Material and methods for the description of biology). It was the most abundant herbivore in these rearings (Tables 1 & 2).

Observations: Eckerö, Kyrkoby (6700:3091) 3 ♂ 3 ♀ 30.VII.2009; Finström, Rågetsböle (6705:3107) 3 ♂ 2 ♀ 1.VIII.2009; Finström, Stålsby (6713:3111) rare 12.VI.2000; Finström, Torrbolstad (6705:3108) 3 ♂ 6 ♀ 1.VIII.2009, (6706:3108) 1 ind. 6 ♀ 1.VIII.2009; Föglö, Finholma (6678:3138) 1 ♂ 2 ♀ 4.VIII.2009; Föglö, Flisö (6674:3128) 7 ♂ 7 ♀ 4.VIII.2009, 11 ♂ 710.X.2011, (6674:3129) 61 ♂ 83 ♀ 4.VIII.2009; Föglö, Hummersö (6672:3129) 9 ♂ 7 ♀ 4.VIII.2009, (6672:3130) 4 ♂ 3 ♀ 4.VIII.2009, (6673:3129) 2 ♂ 4.VIII.2009, (6673:3130) 19 ♂ 15 ♀ 4.VIII.2009; Föglö, Kallsö (6672:3130) 8 ♂ 11 ♀ 4.VIII.2009, (6672:3131) 14 ♂ 17 ♀ 4.VIII.2009; Föglö, Prästgården (6673:3133) 2 ♂ 1 ind. 4.VIII.2009; Föglö, Österön (6682:3142) 3 ind. 3.VIII.2000; Föglö, Överö (6682:3140) 6 ind. 3.VIII.2000, 11 ind. 1.VIII.2001, 17 ♂ 15 ♀ 4.VIII.2009, (6682:3141) 104 ind. 3.VIII.2000, 1 ♂ 10.X.2011, (6683:3138) 33 ♂ 30 ♀ 4.VIII.2009, 2 ♀ 10.X.2011, (6683:3139) 33 ind. 3.VIII.2000, 79 ind. 1.VIII.2001, 41 ♂ 44 ♀ 4.VIII.2009, (6683:3140) 3 ind. 3.VIII.2000, 9 ind. 1.VIII.2001, 51 ♂ 33 ♀ 2 ind. 4.VIII.2009, (6684:3139) 1 ind. 1.VIII.2001; Geta, Dånö (6720:3102) 3 ♂ 8.VIII.2009; Hammarland, Bondtorp (6693:3099) 2 ♂ 1.VIII.2009; Hammarland, Strömma (6709:3101) 1 ♂ 31.VII.2009, (6710:3101) 1 ind. 20.VII.2012; Hammarland, Äspholm (6711:3101) 1

♂ 1 ♀ 31.VII.2009; Hammarland, Östanträsk (6692:3100) 5 ♂ 6 ♀ 1.VIII.2009; Jomala, Brändö (6688:3104) 6 ♂ 6 ♀ 2.VIII.2009; Jomala, Gottby (6688:3100) 2 ♀ 3.VIII.2009; Jomala, Kungsö (6687:3102) 7 ♂ 1 ♀ 3.VIII.2009, (6688:3102) 1 ♂ 2 ♀ 3.VIII.2009, (6688:3103) 1 ♀ 3.VIII.2009; Jomala, Västerkalmare (6688:3110) 2 ♀ 29.VII.2009, (6689:3110) 4 ♀ 29.VII.2009, 3 ind. 21.VII.2012; Jomala, Önningeby (6686:3111) 3 ind. 1.VIII.2000, 15 ind. 30.–31.VII.2001, 1 ♂ 1 ♀ 30.VII.2009, (6686:3113) 10 ind. 1.VIII.2000, 11 ind. 30.–31.VII.2001, (6687:3111) 8 ind. 1.VIII.2000, 26 ind. 30.–31.VII.2001, 18 ♂ 19 ♀ 30.VII.2009, 15 ind. 21.VII.2012, (6687:3112) quite abundant 9.VI.2000, rare 13.VI.2000, quite abundant 3.VII.2000, 25 ind. 1.VIII.2000, 12 ind. 30.–31.VII.2001, 17 ♂ 25 ♀ 30.–31.VII.2009, (6688:3111) abundant 13.VI.2000, 2 ind. 1.VIII.2000, 1 ind. 30.–31.VII.2001, 28 ♂ 25 ♀ 31.VII.2009, (6688:3112) 1 ind. 1.VIII.2000, 2 ind. 30.–31.VII.2001, 66 ♂ 54 ♀ 31.VII.2009, 1 ♂ 3 ♀ 9.X.2011, (6688:3113) 2 ♀ 30.VII.2009; Jomala, Österkalmare (6688:3111) 1 ♂ 30.VII.2009, (6689:3110) 3 ♂ 5 ♀ 29.VII.2009, (6690:3110) 2 ♂ 2 ♀ 29.VII.2009; Kökar, Hamnö (6664:3158) 1 ind. 30.III.2012; Kökar, Hellsö (6664:3162) rare 4.VII.2000; Kökar, Munkvärvan (6663:3158) 1 ♂ 30.III.2012; Kökar, Österbygge (6662:3163) quite abundant 4.VII.2000; Lemland, Flaka (6675:3119) 1 ♂ 2 ♀ 2.VIII.2009, (6675:3120) 1 ♂ 2 ♀ 2.VIII.2009, (6676:3118) 6 ♂ 6 ♀ 2.VIII.2009, (6676:3119) 11 ♂ 14 ♀ 2.VIII.2009, (6676:3120) 2 ♂ 2 ♀ 2.VIII.2009, (6677:3119) 9 ♂ 12 ♀ 2.VIII.2009; Lemland, Granö (6676:3108) 7 ♂ 4 ♀ 8.VIII.2009; Lemland, Järsö (6676:3109) 7 ♂ 6 ♀ 8.VIII.2009, (6676:3110) 12 ♂ 11 ♀ 8.VIII.2009, 1 ♂ 9.X.2011, 4 ind. 21.VII.2012, (6677:3110) 10 ♂ 8 ♀ 8.VIII.2009, 49 ind. 21.VII.2012; Lemland, Lemböte (6683:3111) quite abundant 8.VI.2000, quite abundant 3.VII.2000; Lemland, Näsen (6673:3120) 1 ♂ 1 ♀ 2.VIII.2009; Lemland, Skedholm (6677:3109) 10 ♂ 11 ♀ 8.VIII.2009; Lemland, Vessingsboda (6677:3120) 5 ♂ 5 ♀ 2.VIII.2009, (6678:3120) 22 ♂ 18 ♀ 2.VIII.2009, (6679:3120) 2 ♂ 2 ♀ 2.VIII.2009; Lumparland, Klemetsby (6686:3126) abundant 8.VI.2000, abundant 30.VI.2000, 1 ind. 2.VIII.2000; Lumparland, Krokstad (6682:3124) 1 ♂ 5 ♀ 7.VIII.2009, (6683:3125) 7 ♂ 7 ♀ 7.VIII.2009; Lumparland, Svinö (6681:3125) 31 ♂ 32 ♀ 7.VIII.2009, 16 ind. 21.VII.2012, (6682:3124) 2 ♂ 2 ♀ 8.VIII.2009, (6682:3125) 19 ♂ 15 ♀ 8.VIII.2009, 11 ind. 21.VII.2012; Saltvik, Nääs (6710:3114) rare 9.VI.2000; Sund, Finby (6698:3122) 6 ♂ 5.VIII.2009, (6699:3122) 1 ♂ 1 ♀ 2.VIII.2009; Sund, Kulla (6701:3116) 1 ind. 20.VII.2012; Vårdö, Bussö (6690:3130) 1 ind. 7.VIII.2009.

We have also reared: 39 ♂ 32 ♀ Sa: Lappeenranta, Joutseno, Pellisenranta (6785:3589) 23.VII.2011 (pasture/meadow); 7 ♂ 23 ♀ Sa: Taipalsaari, Vehkataipale (6782:3565) 23.VII.2011 (dry rocky meadow); 32 ♂ 45 ♀ Sa: Taipalsaari, Märkälä (6783:3564) 23.VII.2011 (grazed dry rocky meadow); 7 ♂ 8 ♀ Sa: Taipalsaari, Toija (6784:3560) 23.VII.2011 (dry rocky meadow); 73 ♂ 104 ♀ Sa: Taipalsaari, Jauhiala (6783:3559) 23.VII.2011 (dry rocky meadow); and 43 ♂ 40 ♀ from Sa: Savitaipale, Kärnäkosken linnoitus (6794:3538) 23.VII.2011 (pasture/meadow).

### Ceutorhynchinae

#### *Trichosirocalus troglodytes* (Fabricius, 1787)

A monophagous species on *P. lanceolata* that feeds mainly on the meristem in the caudex and occasionally within the flower stems as a larva (Linders *et al.* 1995). Pupation takes place in the ground close to the host plant. Adults feed on *P. lanceolata* leaves causing characteristic window-like feeding marks with the mesophyll eaten but the upper and lower epidermis remaining intact (naturally with a minuscule penetration hole; Linders *et al.* 1995). It overwinters as an adult, and egg-laying takes place in late spring and early summer (Scherf 1964, Linders *et al.* 1995). In a study in The Netherlands, it was observed that throughout the season a varying, but high proportion (60–100%) of individuals had no flight muscles (Linders *et al.* 1995).

Observations: Finström, Rågetsböle (6705:3107) 1 ind. 1.VIII.2009; Finström, Stålsby (6713:3111) 1 ind. 12.VI.2000; Föglö, Överö (6683:3139) 1 ind. 3.VIII.2000; Jomala, Önningeby (6688:3112) 1 ind. 13.VI.2000; Lemland, Granboda (6682:3122) 1 ind. 1.–30.IV.2009; Lemland, Lemböte (6683:3111) 1 ind. 8.VI.2000; Sund, Bomarsund (6697:3124) 1 ind. 5.VIII.2009.

## A2. Diptera

### Cecidomyiidae

#### *Clinodiplosis cilicrus* (Kieffer, 1889)

New to Finland. Larvae are phytosaprophagous and mycetophagous, and develop in decaying matter of various plant species from several families (Skuhrová 1973, Roskam 1979). They have been found in dry flower-heads of Asteraceae, in withering flowers, in various fruits, and in galls of other gall midges and other insects (Skuhrová 1973), also feeding on damaged plant tissue in galls of other gall midge species in catkins of *Betula* (Roskam 1979). According to Roskam (1979), final instar larvae hibernate in the soil or sometimes in catkins. However, in our rearings they emerged without diapause.

Observations: Föglö, Kallsö (6672:3131) 1 ♂ 4.VIII.2009; Hammarland, Samuelstorp (6696:3098) 1 ♂ 1.VIII.2009; Lemland, Vessingsboda (6678:3120) 1 ♂ 2.VIII.2009; Lumparland, Svinö (6682:3124) 1 ♂ 7.VIII.2009; Sund, Bomarsund (6697:3125) 1 ♂ 3.VIII.2009.

#### *Lestodiplosis* sp.

Some *Lestodiplosis* species are considered specialists but many are generalists (Roskam 1979, Skuhrová & Dengler 2001). Larvae are predatory and attack primarily other gall midge larvae, but apparently also larvae of gall midge parasites and other small insects, in flower-heads, flowers, galls and corresponding places on plants (Roskam 1979, Skuhrová & Dengler 2001). Species of this genus may have several generations a year (Skuhrová & Dengler 2001). According to Roskam (1979), final instar larvae hibernate in the soil or sometimes in catkins. However, in our rearings they emerged without diapause.

Observations: Föglö, Prästgården (6673:3133) 1 ♀ 4.VIII.2009; Föglö, Överö (6682:3140) 1 ♀ 4.VIII.2009, (6683:3139) 2 ♀ 4.VIII.2009, (6683:3140) 1 ♂ 4.VIII.2009; Jomala, Österkalmare (6690:3110) 2 ♀ 29.VII.2009; Lemland, Flaka (6675:3120) 1 ♀ 2.VIII.2009, (6676:3118) 1 ♀ 2.VIII.2009, (6676:3120) 1 ♂ 2.VIII.2009; Lemland, Vessingsboda (6678:3120) 1 ♂ 1 ♀ 1.–2.VIII.2009; Lumparland, Svinö (6681:3125) 2 ♀ 7.VIII.2009; Sund, Bomarsund (6697:3124) 2 ♂ 5.VIII.2009.

### Agromyzidae

#### \**Phytomyza plantaginis* Robineau-Desvoidy, 1851

An oligophagous species mining *Plantago* spp. (mainly leaves), particularly *P. lanceolata* and *P. major* (Spencer 1976). However, all individuals reared in this study emerged from the upper part of the flower stem, as no leaves were included in the samples. Such individuals used to be considered a separate species, *P. plantaginicaulis* Hering, 1944, but it has later been synonymized with *P. plantaginis* (Spencer 1976). Pupation takes place at the end of the mine (Hering 1957, Spencer 1976). According to Hering (1957), *P. plantaginis* has several generations with adults from May to October (but the form *plantaginicaulis* in May and July [in Central Europe and Great Britain]).

Observations: Föglö, Ulversö (6682:3141) 3 ♂ 3.VIII.2000, 2 ind. 3.VIII.2001; Föglö, Överö (6683:3139) 4 ind. 3.VIII.2001, 1 ind. 4.VIII.2009, (6683:3140) 4 ind. 3.VIII.2001; Jomala, Önningsby (6687:3112) 2 ind. 1.VIII.2001, (6688:3111) 2 ind. 31.VII.2009; Jomala, Västansunda (6693:3102) 1 ind. 3.VIII.2009; Lemland, Flaka (6676:3118) 1 ind. 2.VIII.2009; Sund, Bomarsund (6697:3124) 2 ind. 5.VIII.2009.



### A3. Hymenoptera

Platygastroidea

Scelionidae: Telenominae

*Telenomus* sp.

Several species of this genus develop in eggs of Lepidoptera species and some in eggs of shield bugs (Hemiptera: Pentatomoidea) (Kozlov & Kononova 1983). Eggs of shield bugs were probably present in some samples, as their (small) nymphs were quite regularly encountered (see section A4).

*Telenomus chloropus* (Thomson, 1860)

Attacks eggs of Hemiptera: Pentatomoidea. Kozlov and Kononova (1983) and Doğanlar (2001) list the following species as hosts: *Aelia furcula* Fieb., *A. rostrata* Boh., *Carpocoris fuscispinus* Boh., *Dolycoris baccarum* L., *Eurygaster integriceps* Put., *E. austriaca* Schrank, *E. maura* L., *Eysarcoris ventralis* Westw., *Graphosoma lineatum* L., *Palomena prasina* L., *P. viridissima* Poda, *Piezodorus rubrofasciatus* Fabr., *Rhaphigaster nebulosa* (Poda) and *Scotinophara lurida* Burm. It competes with *Trissolcus grandis* as a primary parasitoid (Bulesa 1996) or may act as a hyperparasitoid attacking *T. grandis* (Kozlov 1988, Doğanlar 2001).

Observations: Hammarland, Strömman (6709:3101) 2 ♀ 31.VII.2009; Sund, Finby (6698:3122) 1 ♀ 5.VIII.2009.

*Trissolcus* sp.

Species of this genus parasitize eggs of Hemiptera: Pentatomoidea (Kozlov & Lê 1988).

*Trissolcus grandis* Thomson, 1860

Parasitizes eggs of Hemiptera: Pentatomoidea. Kozlov and Kononova (1983) and Kozlov and Lê (1988) list the following species as hosts: *Aelia acuminata* L., *A. cognata* Fieb., *A. germari* Kuester, *Carpocoris pudicus* Poda, *Dolycoris baccarum* L., *Eurydema ventralis* Kol., *Eurygaster integriceps* Put., *E. austriaca* Schrank, *E. maura* L., *Palomena prasina* L. and *Rhaphigaster nebulosa* (Poda).

Observations: Hammarland, Strömman (6710:3101) 2 ♂ 12 ♀ 31.VII.2009; Jomala, Önningsby (6688:3111) 2 ♂ 31.VII.2009.

Cynipoidea

Figitidae: Charipinae

*Alloxysta* sp.

Hyperparasitoids of Hemiptera: Aphidoidea via primary parasitoids belonging to Aphidiinae (Braconidae) or Aphelinidae (Chalcidoidea) (Gauld & Bolton 1988).

Chalcidoidea

Eulophidae: Entedoninae

\**Chrysocharis pubicornis* (Zetterstedt, 1838)

A solitary endoparasitoid of Diptera: Agromyzidae mainly attacking pupae, but occasionally also larvae (Hansson 1985).

Observations: Föglö, Österön (6682:3141) 2 ♀ 1.VIII.2001; Föglö, Överö (6683:3139) 5 ♀ 1.VIII.2001; Jomala, Önningsby (6687:3112) 1 ♂ 1 ♀ 30.–31.VII.2001; Lemland, Vessingsboda (6678:3120) 1 ♀ 2.VIII.2009.

\**Neochrysocharis formosa* (Westwood, 1833)

A polyphagous species attacking many insect hosts, mainly leaf-mining insects and eggs of sawflies. It has been reared from mines of Diptera: Agromyzidae (Hansson 1990).

Observations: Föglö, Överö (6683:3139) 1 ♂ 1 ♀ 1.VIII.2001, (6683:3140) 1 ♀ 1.VIII.2001; Hammarland, Skarpnåto (6712:3100) 1 ♂ 31.VII.2009.

\**Pediobius metallicus* (Nees, 1834)

A primary, sometimes secondary, solitary endoparasitoid of larvae and pupae of mining Lepidoptera and Diptera, including Agromyzidae (Bouček 1965, Tryapitsyn 1988).

Observations: Föglö, Ulversö (6682:3141) 1 ♀ 3.VIII.2000; Föglö, Överö (6683:3139) 1 ♂ 1.VIII.2001; Hammarland, Strömma (6709:3101) 1 ♀ 31.VII.2009; Lemland, Järsö (6676:3109) 1 ♀ 8.VIII.2009; Lumparland, Svinö (6682:3125) 1 ♂ 7.VIII.2009; Sund, Finby (6698:3121) 1 ♀ 5.VIII.2009, (6699:3122) 1 ♂ 5.VIII.2009.

Eulophidae: Eulophinae

*Sympiesis gregori* Bouček, 1959

Hosts are mainly Lepidoptera: Gracillariidae leaf-miners, including *Aspilapteryx limosella* (Duponchel) and *Aspilapteryx* sp. (Bouček 1959, Storozheva 1981, Noyes 2013). Therefore, the most likely host in Åland is *Aspilapteryx tringipennella* (Zeller) which is a monophagous leaf-miner on *P. lanceolata*.

Observations: Hammarland, Sälis (6704:3098) 2 ♀ 15.VI.2000; Lumparland, Klemetsby (6686:3126) 2 ♂ 30.VI.2000 (reared from *P. lanceolata* leaf-rolls).

Eulophidae: Tetrastichinae

*Aprostocetus* sp. (*lycidas* [Walker, 1839] group), *Aprostocetus* sp.2, *Aprostocetus* sp.3

Species of *Aprostocetus lycidas*-group attack most often Diptera: Cecidomyiidae, rarely also Diptera: Agromyzidae, occasionally leaf-mining Lepidoptera or Coleoptera, and rarely other Coleoptera or parasitic Hymenoptera (Graham 1987). In these rearings, probable hosts were Cecidomyiidae species.

\**Baryscapus endemus* (Walker, 1839)

This species has been reared “from heads of *P. lanceolata*” in Czechoslovakia and England, but the host remained unknown (Graham 1991). It is usually considered a hyperparasitoid (Graham 1991), and the list of associates includes species of Hymenoptera: Pteromalidae (e.g. *Mesopolobus subfumatus* [Ratzeburg], *Pteromalus* sp.) (Noyes 2013). In this community, it highly likely parasitizes *M. incultus*.

Observations: Eckerö, Kyrkoby (6700:3091) 3 ♀ 30.VII.2009; Finström, Rågetsböle (6705:3107) 7 ♀ 1.VIII.2009; Finström, Torrbolstad (6705:3108) 11 ♀ 1.VIII.2009, (6706:3108) 5 ♀ 1.VIII.2009; Föglö, Flisö (6674:3128) 1 ♀ 4.VIII.2009, (6674:3129) 1 ♂ 17 ♀ 4.VIII.2009; Föglö, Hummersö (6673:3130) 2 ♀ 4.VIII.2009; Föglö, Kallsö (6672:3131) 2 ♀ 4.VIII.2009; Föglö, Prästgården (6673:3133) 1 ♀ 4.VIII.2009; Föglö, Österön (6682:3141) 27 ♂ 4 ♀ 1.VIII.2001; Föglö, Överö (6682:3140) 29 ♀ 4.VIII.2009, (6683:3138) 44 ♀ 4.VIII.2009, (6683:3139) 1 ♀ 3.VIII.2000, 109 ♂ 20 ♀ 1.VIII.2001, 25 ♀ 4.VIII.2009, (6683:3140) 43 ♀ 4.VIII.2009, (6684:3139) 15 ♂ 1 ♀ 1.VIII.2001, (6684:3140) 1 ♀ 4.VIII.2009; Geta, Dånö (6720:3102) 3 ♀ 8.VIII.2009; Hammarland, Äspholm (6712:3101) 1 ♀ 31.VII.2009; Hammarland, Östanträsk (6692:3100) 1 ♀ 1.VIII.2009; Jomala, Kungsö (6687:3102) 4 ♀ 3.VIII.2009; Jomala, Västerkalmare (6688:3110) 2 ♀ 30.VII.2009, (6689:3110) 1 ♀ 29.VII.2009; Jomala, Önningsby (6686:3113) 12 ♂ 1 ♀ 30.–31.VII.2001, (6687:3111) 8 ♂ 1 ♀ 30.–31.VII.2001, 20 ♀ 1.VIII.2009, (6687:3112) 2 ♂ 5 ♀ 30.VII.2009, (6688:3111) 1 ♂ 18 ♀ 31.VII.2009, (6688:3112) 1 ♀ 31.VII.2009, (6688:3113) 1 ♀ 30.VII.2009; Jomala, Österkalmare (6690:3110) 8 ♀ 29.VII.2009; Lemland, Flaka (6676:3119) 4 ♀ 2.VIII.2009; Lemland, Granö (6676:3108) 4 ♀ 8.VIII.2009; Lemland, Järsö (6676:3109) 19 ♀ 8.VIII.2009, (6676:3110) 3 ♀ 8.VIII.2009, (6677:3109) 5 ♀ 8.VIII.2009; Lemland, Skedholm (6677:3109) 19 ♀ 8.VIII.2009; Lemland, Vessingsboda (6677:3120) 1 ♀ 2.VIII.2009, (6678:3120) 2 ♂ 11 ♀ 2.VIII.2009; Lumparland, Svinö (6681:3125) 11 ♀ 7.VIII.2009, (6682:3125) 10 ♀ 7.VIII.2009; Sund, Finby (6699:3122) 1 ♀ 2.VIII.2009.

We have also reared: 1 ♀ Sa: Savitaipale, Kärnäkosken linnoitus (6794:3538) 23.VII.2011 (a pasture/meadow); and 2 ♀ Sa: Taipalsaari, Jauhiala (6783:3559) 23.VII.2011 (a dry rocky meadow); both sites had *M. pascuorum* population.

### Eupelmidae: Eupelminae

#### \**Eupelmus vesicularis* (Retzius, 1783)

A highly generalist species with brachypterous females acting as both a primary and a hyperparasitoid (i.e. omnivorous). It has a very long list of associates, including Coleoptera: Curculionidae (e.g. *Gymnetron* sp., *Mecinus collaris* Germar), Diptera: Cecidomyiidae and Hymenoptera: Pteromalidae (Bouček 1977, Noyes 2013). Kruess and Tscharrntke (2000) list *Oxystoma ochropus* (Germar) (Coleoptera: Apionidae) as the only host in a community of herbivorous and parasitoid insects feeding on *Vicia sepium*. According to Gibson (1995) it is a superior competitor of other parasitoids: its “enhanced abilities to develop on diverse hosts within a similar microhabitat, to develop readily either as a primary parasite or as a hyperparasitoid, and to kill other parasitoids attacking the same host could enhance the evolutionary success of a species by compensating for a lesser ability to disperse and colonize new host populations than competitors”. It was the second most abundant parasitoid species in rearings (Tables 1 & 2). It probably attacks both *M. incultus* and *M. pascuorum*, and possibly also other species occurring in spikes.

Observations: Eckerö, Kyrkoby (6700:3091) 1 ♂ 30.VII.2009; Finström, Rågetsböle (6705:3107) 3 ♂ 8 ♀ 1.VIII.2009; Finström, Torrbolstad (6705:3108) 4 ♂ 5 ♀ 1.VIII.2009, (6706:3108) 2 ♂ 7 ♀ 1.VIII.2009; Föglö, Finholma (6678:3138) 3 ♂ 2 ♀ 4.VIII.2009; Föglö, Flisö (6674:3128) 32 ♂ 17 ♀ 4.VIII.2009, (6674:3129) 63 ♂ 52 ♀ 4.VIII.2009; Föglö, Hummersö (6672:3129) 11 ♂ 16 ♀ 4.VIII.2009, (6672:3130) 4 ♂ 9 ♀ 4.VIII.2009, (6673:3130) 38 ♂ 26 ♀ 4.VIII.2009; Föglö, Kallsö (6672:3130) 4 ♂ 5 ♀ 4.VIII.2009, (6672:3131) 4 ♂ 4 ♀ 4.VIII.2009; Föglö, Ulversö (6682:3141) 1 ♂ 4 ♀ 1.VIII.2001; Föglö, Österön (6682:3141) 13 ♂ 5 ♀ 1.VIII.2001; Föglö, Överö (6682:3140) 8 ♂ 17 ♀ 4.VIII.2009, (6682:3141) 2 ♀ 3.VIII.2000, (6683:3138) 45 ♂ 62 ♀ 4.VIII.2009, (6683:3139) 6 ♀ 3.VIII.2000, 10 ♂ 20 ♀ 1.VIII.2001, 90 ♂ 84 ♀ 4.VIII.2009, (6683:3140) 1 ♂ 1 ♀ 3.VIII.2000, 1 ♂ 1.VIII.2001, 54 ♂ 73 ♀ 4.VIII.2009, (6684:3139) 2 ♀ 1.VIII.2001, (6684:3140) 8 ♂ 5 ♀ 4.VIII.2009; Geta, Dänö (6720:3102) 3 ♂ 1 ♀ 8.VIII.2009; Hammarland, Strömma (6710:3101) 1 ♂ 31.VII.2009; Hammarland, Äspholm (6711:3101) 1 ♂ 1 ♀ 31.VII.2009, (6712:3101) 1 ♀ 31.VII.2009; Hammarland, Östanträsk (6692:3100) 2 ♂ 3 ♀ 1.VIII.2009; Jomala, Brändö (6688:3104) 7 ♂ 3 ♀ 2.VIII.2009; Jomala, Kungsö (6687:3101) 2 ♂ 7 ♀ 3.VIII.2009, (6687:3102) 6 ♂ 10 ♀ 3.VIII.2009, (6688:3102) 1 ♂ 1 ♀ 3.VIII.2009; Jomala, Västerkalmare (6688:3110) 1 ♂ 6 ♀ 29.–30.VII.2009, (6689:3110) 1 ♂ 1 ♀ 29.VII.2009; Jomala, Önningeby (6686:3111) 1 ♀ 30.VII.2009, (6686:3113) 1 ♂ 1.VIII.2000, 4 ♂ 5 ♀ 30.–31.VII.2001, (6687:3111) 1 ♂ 1 ♀ 1.VIII.2000, 14 ♂ 7 ♀ 31.VII.2009, (6687:3112) 4 ♂ 6 ♀ 30.–31.VII.2001, 9 ♂ 22 ♀ 30.–31.VII.2009, 1 ind. 21.VII.2012, (6688:3111) 1 ♀ 30.–31.VII.2001, 3 ♂ 14 ♀ 31.VII.2009, (6688:3112) 2 ♀ 1.VIII.2000, 1 ♂ 2 ♀ 30.–31.VII.2001, 7 ♂ 14 ♀ 30.–31.VII.2009; Jomala, Österkalmare (6690:3110) 2 ♂ 1 ♀ 29.VII.2009; Lemland, Flaka (6675:3119) 2 ♂ 1 ♀ 2.VIII.2009, (6675:3120) 5 ♂ 9 ♀ 2.VIII.2009, (6676:3118) 1 ♂ 1 ♀ 2.VIII.2009, (6676:3119) 24 ♂ 26 ♀ 2.VIII.2009, (6676:3120) 1 ♀ 2.VIII.2009, (6677:3119) 7 ♂ 11 ♀ 2.VIII.2009; Lemland, Granö (6676:3108) 11 ♂ 12 ♀ 8.VIII.2009; Lemland, Järsö (6676:3109) 12 ♂ 5 ♀ 8.VIII.2009, (6676:3110) 15 ♂ 14 ♀ 8.VIII.2009, (6677:3109) 6 ♂ 3 ♀ 8.VIII.2009, 1 ind. 21.VII.2012; Lemland, Skedholm (6677:3109) 9 ♂ 5 ♀ 8.VIII.2009; Lemland, Vessingsboda (6677:3120) 7 ♂ 1 ♀ 2.VIII.2009, (6678:3120) 27 ♂ 33 ♀ 1.–2.VIII.2009; Lumparland, Krokstad (6682:3124) 9 ♂ 6 ♀ 7.VIII.2009, (6683:3125) 12 ♂ 13 ♀ 7.VIII.2009; Lumparland, Svinö (6681:3125) 25 ♂ 58 ♀ 7.VIII.2009, 1 ind. 21.VII.2012, (6682:3124) 3 ♂ 2 ♀ 7.VIII.2009, (6682:3125) 24 ♂ 29 ♀ 8.VIII.2009; Sund, Bomarsund (6696:3125) 1 ♂ 1 ♀ 3.VIII.2009, (6697:3124) 1 ♀ 5.VIII.2009; Sund, Finby (6699:3122) 2 ♀ 2.VIII.2009; Vårdö, Östra Simskåla (6710:3133) 1 ♀ 6.VIII.2009.

We have also reared: 1 ♀ Sa: Savitaipale, Kärnäkosken linnoitus (6794:3538) 23.VII.2011 (a pas-

ture/meadow); and 2 ♂ Sa: Taipalsaari, Vehkataipale (6782:3565) 23.VII.2011 (a dry rocky meadow); both sites had *M. pascuorum* population, Savitaipale also *M. incultus* population.

#### Mymaridae

##### *Polynema* sp.

Species of this genus have been reared as primary parasitoids of eggs of Coleoptera: Curculionidae (*Anthonomus* spp.) and Hemiptera: Cicadellidae, Miridae and Nabidae (Noyes 2013).

#### Pteromalidae: Miscogastrinae

##### \**Thinodytes cyzicus* (Walker, 1839)

It has been reared from leaf mines of Diptera: Agromyzidae, e.g. *Chromatomyia horticola* (Goureau) (Kamijo 1978).

Observations: Föglö, Överö (6683:3139) 1 ♂ 1.VIII.2001, (6683:3140) 1 ♂ 1.VIII.2001.

#### Pteromalidae: Pteromalinae

##### *Mesopolobus* sp.

At least some of these individuals may be *M. mediterraneus* (Mayr, 1903), which is a generalist species attacking e.g. larvae of Coleoptera: Apionidae and Chrysomelidae, Bruchinae (Graham 1969).

##### \**Mesopolobus incultus* (Walker, 1834)

The most abundant parasitoid species in the rearings (Tables 1 & 2; Vikberg & Nieminen 2012). It has been reared by Rosen (1961) from flower-heads of *Trifolium pratense* L. together with some *Apion s.l.* (Coleoptera: Apionidae) and a pteromalid *Spintherus obscurus* Thomson (currently the valid name is *S. dubius* [Nees, 1834]). According to Rosen (1961), *M. incultus* was likely the host of *S. obscurus*. Later many individuals of *M. incultus* have been reared from flower-heads of *Trifolium repens* L. as a primary parasitoid of *Apion flavipes* Hoffmann (currently *Protapion fulvipes* [Geoffroy]; wasp larvae were observed on host larvae) in Skåne, southern Sweden (Rosen 1962). Furthermore, it is known to be a solitary parasitoid of *M. pascuorum* (Mohd Norowi *et al.* 2000, Baur *et al.* 2007, Hancock *et al.* 2013, Herbst *et al.* 2013), and possibly also of some other *Apion s.l.* and *Mecinus* species (Graham 1969). *Mecinus labilis* (Herbst) is also a likely host (Hancock *et al.* 2013, Herbst *et al.* 2013; Torsten Meiners, pers. comm.). However, we suppose that the interpretation that *M. incultus* is highly generalist results from inaccurate host information in older records, especially records from other orders than Coleoptera are highly dubious based on our rearings and data in the recent literature (e.g. Baur *et al.* 2007). Moreover, preliminary DNA-barcoding results strongly indicate that *M. incultus* individuals reared from *P. lanceolata* and *T. repens* represent separate species (Gergely Várkonyi, unpublished). Recently, it has been found that *M. incultus* is attracted by both host plant and *M. pascuorum* host volatiles (Wäschke *et al.* 2014).

Observations since Vikberg and Nieminen (2012): Jomala, Önningeby (6687:3111) 6 ind. 21.VII.2012, (6688:3112) 4 ind. 21.VII.2012; Lemland, Järsö (6676:3110) 1 ind. 21.VII.2012, (6677:3109) 40 ind. 21.VII.2012, (6677:3110) 3 ind. 21.VII.2012; Lumparland, Svinö (6681:3125) 13 ind. 21.VII.2012; Sund, Färjsundet (6701:3113) 3 ind. 20.VII.2012; Sund, Finby (6697:3123) 1 ind. 20.VII.2012; Sund, Kulla (6701:3116) 1 ind. 20.VII.2012.

##### *Pteromalus* sp.

A very large genus including primary and hyperparasitoids of arthropods from specialists to highly generalist species (Noyes 2013).

We have also reared: 2 ♀ Sa: Taipalsaari, Märkälä (6783:3564) 23.VII.2011 (a pasture/dry rocky meadow); 2 ♂ Sa: Taipalsaari, Vehkataipale (6782:3565) 23.VII.2011 (a dry rocky meadow); and 1 ♂ Sa: Taipalsaari, Jauhiala (6783:3559) 23.VII.2011 (a dry rocky meadow); all sites had *M. pascuorum* population.

\**Pteromalus (Habrocytus) semotus* (Walker, 1834)

A primary and a hyperparasitoid of many Lepidoptera species and their parasitoids (e.g. two *Baryscapus* species), but it has also been associated with Coleoptera (e.g. Curculionidae) (Noyes 2013). In our rearings it is probably a parasitoid of *M. pascuorum*.

Observations: Föglö, Ulversö (6682:3141) 2 ♂ 3 ♀ 1.VIII.2001; Föglö, Överö (6683:3139) 1 ♂ 2 ♀ 4.VIII.2009; Jomala, Önningeby (6688:3111) 2 ♂ 31.VII.2009.

We have also reared: 5 ♂ 3 ♀ Sa: Savitaipale, Kärnäkosken linnoitus (6794:3538) 23.VII.2011 (a pasture/meadow); 1 ♂ 2 ♀ Sa: Taipalsaari, Vehkataipale (6782:3565) 23.VII.2011 (a dry rocky meadow); and 6 ♂ 10 ♀ Sa: Taipalsaari, Jauhiala (6783:3559) 23.VII.2011 (a dry rocky meadow); all sites had *M. pascuorum* population.

Ichneumonoidea

Ichneumonidae: Cryptinae

*Dichrogaster aestivalis* (Gravenhorst, 1829)

Hosts include several species of Neuroptera: Chrysopidae, e.g. it has been reared from cocoons of *Chrysopa* (Horstmann 1973, Yu 2012). Chrysopidae spp. were present on several spikes when sampling was performed, but they were not sampled nor identified.

Observations: Föglö, Överö (6682:3140) 1 ♀ 3.VIII.2000, (6683:3140) 1 ♂ 1.VIII.2001; Geta, Dånö (6721:3101) 1 ♀ 8.VIII.2009; Sund, Bomarsund (6696:3125) 1 ♂ 3.VIII.2009.

*Gelis* sp.

Many *Gelis* species are pseudohyperparasitoids attacking pupae of hymenopteran parasitoids (Yu 2012). Females are usually apterous.

Braconidae: Aphidiinae

*Aphidius* sp., *Ephedrus* sp., *Trioxys* sp.

All species of this subfamily parasitize Hemiptera: Aphidoidea (Yu 2012). Aphidoidea species did not occur in these samples, but they are relatively common on *P. lanceolata* in Åland (see Nieminen *et al.* 2004). It is also possible that some parasitized aphids have come from other plants nearby and attached on *P. lanceolata* as mummies.

Braconidae: Braconinae

\**Bracon (Glabrobracon) delibator* Haliday, 1833 (= *anthracinus* Nees, 1834)

It has been reared from *Miarus (Gymnetron) campanulae* (Linnaeus) (Coleoptera: Curculionidae) (Yu *et al.* 2005, Yu 2012) and from *P. lanceolata* seedheads in England (Mark Shaw, pers. comm.).

Observations: Föglö, Flisö (6674:3129) 1 ♀ 4.VIII.2009; Föglö, Överö (6682:3140) 1 ♂ 3.VIII.2000, (6683:3138) 1 ♂ 4.VIII.2009, (6683:3139) 2 ♂ 3.VIII.2000, 2 ♂ 1.VIII.2001, 1 ♂ 4.VIII.2009; Geta, Dånö (6721:3101) 1 ♂ 8.VIII.2009; Hammarland, Strömman (6708:3101) 1 ♀ 31.VII.2009; Jomala, Brändö (6688:3104) 1 ♀ 2.VIII.2009; Jomala, Gottby (6688:3100) 1 ♀ 3.VIII.2009; Jomala, Önningeby (6687:3112) 1 ♂ 3.VII.2000, (6688:3112) 1 ♂ 1.VIII.2000; Lemland, Lemböte (6683:3111) 1 ♀; Lumparland, Svinö (6682:3125) 1 ♂ 7.VIII.2009; Vårdö, Bussö (6691:3130) 1 ♂ 7.VIII.2009.

Braconidae: Opiinae

\**Opiinae* sp., *Opius pallipes* Wesmael, 1835, *Phaedrotoma depeculator* Förster, 1862, *Phaedrotoma diversa* (Szépligeti, 1898)

All species in the subfamily Opiinae parasitize Diptera: Agromyzidae. According to Fischer (1967, 1969), *P. depeculator* has been reared from *P. plantaginis* hosts on *P. lanceolata*, and *P. diversa* from *P. plantaginis* hosts (Fischer 1964). *Opius pallipes* has been reared from several genera within

Agromyzidae (Tobias & Jakimavicius 1995) including 12 *Phytomyza* species (Yu 2012). (Some reared individuals are lost, so their identification is not possible [included in Table 1 as Opiinae sp.].)

Observations: *O. pallipes* Föglö, Överö (6683:3139) 1 ♀ 3.VIII.2001; *P. depeculator* Föglö, Österön (6682:3141) 1 ♀ 3.VIII.2001; Hammarland, Skarpnåtö (6712:3100) 1 ♀ 31.VII.2009; *P. diversa* Föglö, Överö (6683:3140) 1 ♀ 3.VIII.2001.

Ceraphronoidea: Ceraphronidae

*Aphanogmus* sp., *Ceraphron* sp.

Some species of these genera have been reared from Diptera: Cecidomyiidae (Alekseev 1988).

## A4. Hemiptera

Three species of shield bugs (Heteroptera: Pentatomidae) were relatively abundant in the samples, most individuals were in the nymphal stage (Table A1). These species mainly feed on various herbs, also on developing seeds of *P. lanceolata* (S. van Nouhuys, pers. comm.), but many shield bugs also act as predators, and *P. lanceolata* is apparently a suitable host for their complete larval development. Two of these three bug species belong to the known hosts of two egg parasitoid species (*T. chloropus* and *T. grandis*) that emerged from the rearings (see above and Tables 1 & 2).

Two further hemipteran species were present in the 2009 samples. The nettle ensign scale (*Orthezia urticae* [Linnaeus]; Coccoidea: Ortheziidae), which is polyphagous, was found from Jomala, Kungsö (6687:3102, 3.VIII.2009), and the leafhopper *Anaceratagallia ?ribauti* (Ossiannilsson) (Membracoidae: Cicadellidae), which probably is polyphagous but is known to feed on *P. lanceolata*, from Sund, Finby (6698:3122, 6.VIII.2009).

## A5. Thysanoptera

Most thrips in the samples were *Haplothrips propinquus* (Table A2). Three samples also included 3–8 exx. of *Haplothrips leucanthemi* and one sample a single *Chirothrips hamatus*. Both *Haplothrips* species are very widespread and abundant in Finland (J. Kettunen, pers. comm.). Larvae of *H. propinquus* mainly feed on *Achillea*, those of *H. leucanthemi* on Asteraceae, and those of *C. hamatus* on Poaceae (Lewis 1973). Some bright-red thysanopteran larvae are frequently abundant on *P. lanceolata* (also on spikes) in Åland. Based on their colouration, they are supposedly some *Haplothrips* species (J. Kettunen, pers. comm.) and, therefore, according to observations mainly represent *H. propinquus*. Adults are much less selective and feed on pollen of various white, yellow and blue flowers (J. Kettunen, pers. comm.).

Table A1. Identified true bugs (Hemiptera: Heteroptera) from the 2009 rearing (collected 29.VII.–8.VIII.2009).

Taxon	No. of patches	No. of inds.
<i>Aelia ?acuminata</i> (Linnaeus) <sup>†</sup>	3	3
<i>Carpocoris purpureipennis</i> (De Geer) <sup>**</sup>	9	10
<i>Dolycoris baccarum</i> (Linnaeus) <sup>**</sup>	12	13 <sup>a</sup>
<i>Eurydema oleraceum</i> (Linnaeus) <sup>***</sup>	1	1
<i>Palomena prasina</i> (Linnaeus) <sup>****</sup>	12	18
Pentatomidae sp.	9	11

Notes. Nomenclature follows Aukema & Rieger (1995–2006).

<sup>†</sup> The only *Aelia* sp. known from Åland, feeds on Poaceae (Rintala & Rinne 2010).

<sup>\*\*</sup> Feeds on various herbs (Rintala & Rinne 2010).

<sup>\*\*\*</sup> Feeds on Brassicaceae (Rintala & Rinne 2010).

<sup>\*\*\*\*</sup> Feeds on various herbs and some woody plants (Rintala & Rinne 2010).

a) One individual on *Plantago media*.

Table A2. Identified thrips (Thysanoptera) samples.

Species	Sampling date	Location
All <i>Haplothrips propinquus</i> Bagnall	15.VI.2000	Hammarland, Sâlis (6704:3098)
All <i>Haplothrips propinquus</i>	9.VI.2000	Saltvik, Nääs (6710:3114)
Mainly <i>Haplothrips propinquus</i> , some <i>Haplothrips leucanthemi</i> (Schrank), one <i>Chirothrips hamatus</i> Trybom	8.VI.2000	Lumparland, Klemetsby (6686:3126)
Mainly <i>Haplothrips propinquus</i> , some <i>Haplothrips leucanthemi</i>	15.VI.2000	Eckerö, Torp (6698:3089)
Mainly <i>Haplothrips propinquus</i> , some <i>Haplothrips leucanthemi</i>	8.VI.2000	Lemland, Lemböte (6683:3111)
All <i>Haplothrips propinquus</i>	9.VI.2000	Jomala, Önningby (6687:3112)

Note. Nomenclature follows Mound (2008).