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How rapidly do invasive birch forest geometrids recruit larval parasitoids? Insights from comparison with a sympatric native geometrid

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Abstract Two related issues in studies of biological invasions are how quickly the enemy complexes of invasive species become as species-rich and efficient as those of native species and how important enemy release is for the establishment and spread of invaders. We addressed these issues for the geometrid moths *Operophtera brumata* and *Agriopis aurantiaria*, who invaded the coastal mountain birch forest of northern Norway by range expansion approximately a century and 15 years ago, respectively. This was done by comparing larval parasitoid species richness and prevalence among the invaders and the native geometrid *Epirrita autumnata*. We found that *E. autumnata* and *O. brumata* both hosted seven parasitoid species groups, whereas *A. aurantiaria* hosted only one.

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Several parasitoid groups were shared between two or more of the geometrids. Total larval parasitism rates were similar in all three geometrid species, and comparison with published studies on larval parasitism in Western Europe suggested that *O. brumata* and *A. aurantiaria* do not suffer lower parasitism rates in our study region than in their native ranges. Our results indicate that accumulation of larval parasitoids on invasive geometrids in coastal mountain birch forest may reach completion within a few decades to at least a century after the invasion, and that establishment and spread of such invaders is unlikely to be facilitated by release from larval parasitism. Our investigations also uncovered a high degree of spatiotemporal synchrony between the total larval parasitism rates of *O. brumata* and *A. aurantiaria*, suggesting that larval parasitism of different geometrid species in the study system is governed by some common external factor.

Keywords *Agriopis* · Altitudinal gradient ·
Enemy release · Geometrid · Invasion ·
Parasitoid · Range expansion

Introduction

Invasions by alien insect species, facilitated by climate change or human introduction, are reported from a growing number of ecosystems worldwide. Understanding the ecological dynamics of such invasions is a challenge (Snyder and Evans 2006; Kenis et al.

2009; Engelkes and Mills 2011). One fundamental question is how rapidly invasive insects recruit effective enemy communities in their invaded ranges. If enemy recruitment is slow, the establishment and spread of invaders can potentially be facilitated by enemy release and there might be increased risk of invaders becoming high-density pests (Torchin et al. 2003; Colautti et al. 2004; Torchin and Mitchell 2004; Roy et al. 2011). Insects generally suffer heavy mortality from parasitoids (Godfray 1994; Quicke 1997), which therefore make particularly suitable model systems for testing these ideas.

It is typically found that invasive insects (i.e., hosts) initially suffer lower parasitism rates and are attacked by fewer parasitoid species in their invaded than native ranges (Cornell and Hawkins 1993; Hawkins and Cornell 1994; Schönrogge et al. 2006; Menéndez et al. 2008; Grabenweger et al. 2010). Thus, release from parasitoids may potentially be important for the establishment and spread of many invasive insects. However, it is largely uncertain how long-lasting such parasitoid release might be. There is evidence that invasive hosts tend to accumulate additional parasitoid species with increasing time since the invasion (Cornell and Hawkins 1993; Hawkins and Cornell 1994), but the speed of this process is not well known. Cornell and Hawkins (1993) and Hawkins and Cornell (1994) suggested that anywhere between 100 and 10,000 years may be needed before the parasitoid complexes of invasive hosts attain a species richness and functionality that is equivalent to the complexes of native hosts. More precise estimates are difficult to obtain, owing to the extensive timescales involved. However, the speed with which an invasive host accumulates parasitoids can sometimes be assessed by comparing its parasitoid complex between areas where it has different residence times (e.g., Schönrogge et al. 1995, 2006). Unfortunately, the results of such biogeographical comparisons can be difficult to interpret due to geographical gradients in parasitoid species richness and/or efficiency, which may affect the parasitoid complex of an invasive host independently of its residence time (Gröbler and Lewis 2008).

An opportunity to implement an alternative approach arises when several alien host species have sequentially invaded a system that was already occupied by a taxonomically and ecologically similar native host species. Parasitoid complexes can then be compared among invasive hosts with different

residence times and a native “reference species” within the same system. This may suggest how rapidly the parasitoid complexes of the invaders are converging to a native level, without the potential problems of comparing different geographical areas. Such within-range comparisons rely on the assumption that the parasitoid complexes of the invasive hosts will eventually become as species-rich and efficient as the complex of the native host (i.e., that the parasitoid complexes of the native and invasive hosts are inherently similar). This assumption is not necessarily justified, since parasitoid complexes can differ substantially even between closely related host species (e.g., Askew 1994). Thus, in order to make inferences about parasitoid accumulation and release in invasive hosts as robust as possible, within-range comparisons between native and invasive hosts should, ideally, be combined with biogeographical comparisons of invasive hosts in their native and invaded ranges.

In the sub-arctic mountain birch forests (*Betula pubescens* ssp. *czerepanovii* Orlova) of northern Fennoscandia, a rare opportunity to implement such a dual comparative approach is provided by a system of three sympatric geometrid moths (Lepidoptera: Geometridae) with contrasting residence times: *Epirrita autumnata* (Bkh.) (Autumnal moth), a native species; *Operophtera brumata* (L.) (Winter moth), an invader from the south that expanded its range into this system about a century ago [first recording near Tromsø (69°40'N) in 1892]; and *Agriopis aurantiaria* (Hübner) (Scarce umber moth), another southern species that invaded by range expansion only about 15 years ago [See Jepsen et al. (2011) for details on geometrid invasions in this system]. Both *O. brumata* and *A. aurantiaria* are well known pests of broad-leaved trees in their native ranges further south in Europe (Kenis et al. 2005; Cross et al. 1999), and their parasitoid complexes in these ranges have been surveyed as part of biological control programs and ecological studies. Thus, this three-species geometrid system offers an excellent opportunity to compare parasitism between native and invasive hosts within the invaded range, as well as between invasive hosts in their native and invaded ranges.

Ongoing monitoring of the three sympatric geometrids in the coastal areas of northern Norway has captured the invasion of *A. aurantiaria* in this region (Jepsen et al. 2011). In the present study, we synthesize the parasitism data gathered throughout the

monitoring period to map and compare the species-composition and prevalence of the larval parasitoid guilds attacking the three geometrids. Moreover, we survey previously published studies on parasitism of *O. brumata* and *A. aurantiaria* in Western Europe to compare the larval parasitoid guilds of these two invaders between their native ranges and our (invaded) study region in northern Norway. Our results allow us to assess how rapidly the larval parasitoid guilds of *O. brumata* and *A. aurantiaria* are approaching native levels of species richness and prevalence and to evaluate the degree to which the establishment and spread of these invaders in the study region might have been facilitated by a release from larval parasitism.

Materials and methods

Study species

Epirrita autumnata and *O. brumata* have a circumpolar distribution, while the distribution of *A. aurantiaria* is Eurasian. Our study region in northern Norway represents the approximate northern distributional limit for all three geometrids in Europe. All three species have a largely similar ecology. In northern Fennoscandia, the larvae feed mainly on mountain birch and pubescent birch (*Betula pubescens* Ehrhart), which are the dominant tree species in the region. Larvae hatch from overwintering eggs in approximate synchrony with birch budburst (occurring in late May to early June in the study region) and subsequently develop through 5 instars. Larval development takes 4–8 weeks, depending on temperature and forage quality, before pupation occurs in the soil in late June to early July. Adult moths eclose in autumn and oviposit in trees. The females of *O. brumata* and *A. aurantiaria* are flightless and dispersal of these species, therefore, occurs mainly by ballooning (wind dispersal with silk threads) of first-instar larvae. *E. autumnata* and *O. brumata* show cyclic population dynamics in coastal northern Norway, with population peaks every 9–10 years (Tenow 1972; Bylund 1999). The population dynamics of *A. aurantiaria* in this system are still poorly known, but appear to resemble the dynamics of the other two geometrids (Jepsen et al. 2011). The three geometrids display large-scale differences in their geographical

distributions within the study system: *E. autumnata* is common in both coastal and continental sections of the sub-arctic mountain birch system, while the two invasive geometrids have so far been restricted mainly to the coast [although there is evidence for recent continental range expansion in *O. brumata* (Jepsen et al. 2008)]. In the coastal regions of Troms County, northern Norway, high-density populations of all three geometrids occur in sympatry.

Species-composition and prevalence of larval parasitoid guilds in the study region

Between 2001 and 2011, we reared parasitoids from geometrid larvae sampled at four locations in Troms County, northern Norway, namely Lyngen (69°20'N, 20°00'E), Skogsfjord (69°55'N, 19°18'E), Storelva (69°38'N, 18°57'E) and Reinøya (70°00'N, 19°49'E) (Fig. 1). Larvae of all three geometrid species were sampled at the same time by shaking birch branches in a large plastic box, thus ensuring that all of the species were sampled from the exact same habitat. Sampling was conducted during the fourth to early fifth larval instar, i.e., after most parasitoid attacks have occurred but before parasitoids have started to eclose from the larvae.

At Storelva, during 2006–2008, we sampled specifically to compare larval parasitism rates between *O. brumata* and *A. aurantiaria*, as this location hosted comparable densities of the two geometrid species (Fig. 2a. Note that *E. autumnata* was rare at Storelva, with hardly any larvae being observed throughout the study period). Because larval parasitism rates and geometrid densities in coastal mountain birch forest can show pronounced altitudinal variation (Hagen et al. 2007; Schott et al. 2010; Vindstad et al. 2011), this sampling was conducted in an altitudinal gradient established as part of a long-term monitoring system for geometrid population dynamics in the study region (Jepsen et al. 2011). The gradient was located within a continuous belt of mountain birch forest, stretching from the sea level to the tree line (≈ 250 m a.s.l.), and had 10–12 sampling stations at each of the altitudes 50, 100, 170 and 240 m.a.s.l. (44 stations in total). The stations within each altitude were arranged as a roughly linear transect and spaced by 200 m intervals. Larval densities were estimated at all stations at approximately the same time as larval sampling. This was done by haphazardly gathering ten 60–80 cm

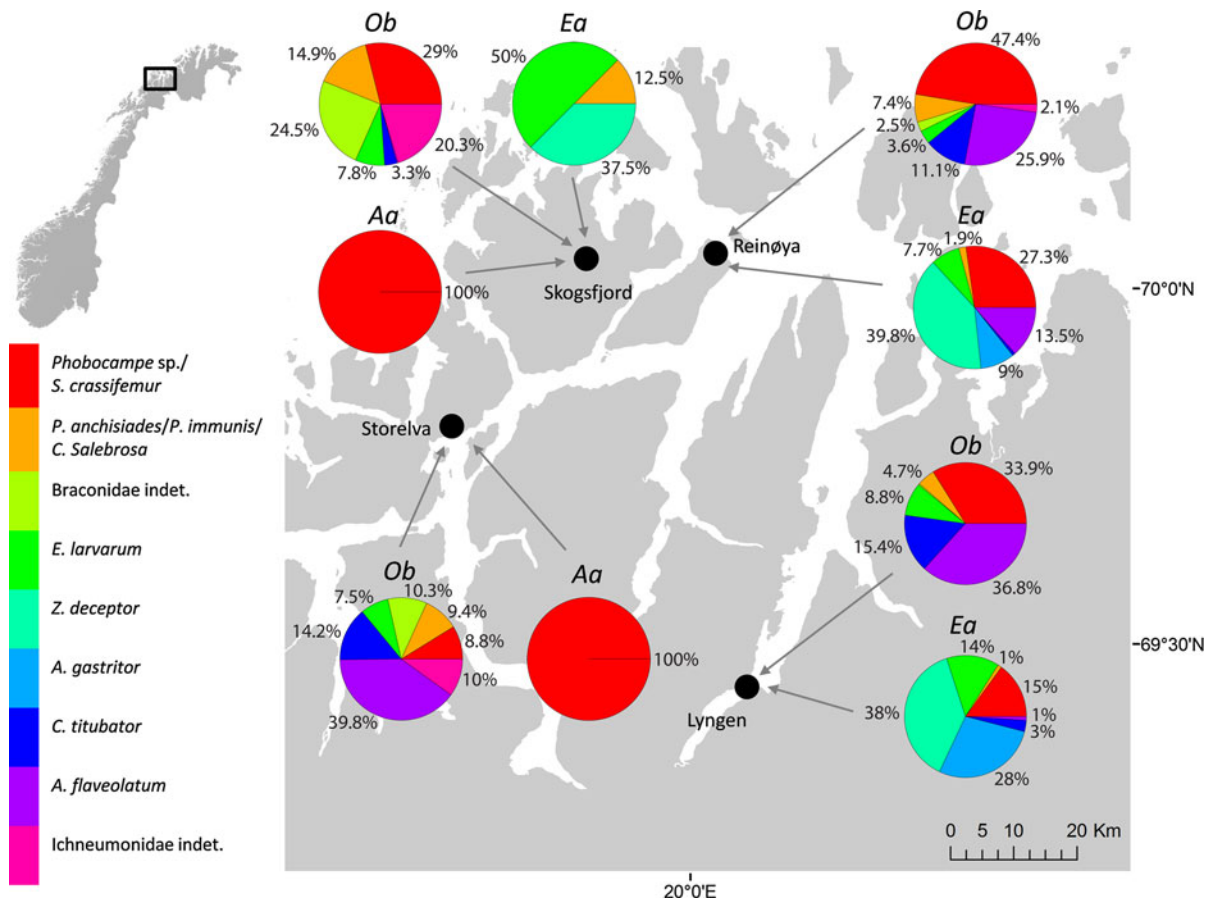


Fig. 1 Map of the study region in Troms County, Northern Norway, with the four sampling locations Lyngen, Skogsfjord, Storelva and Reinøya. Sector diagrams show the proportion of larvae parasitized by each parasitoid species group, out of all

parasitized larvae, for each location and geometrid host species. Proportions of <1 % are not shown. *Aa* *A. aurantiaria*, *Ob* *O. brumata*, *Ea* *E. autumnata*

birch branches within a 30 m radius of the stations, shaking the branches thoroughly in a large plastic box, and counting the number of larvae that were dislodged (Ims et al. 2004).

Sampled larvae were reared in the laboratory following standard procedures, as described in Hagen et al. (2006). Larvae with unexplained mortality or unknown fate were excluded from the data before estimation of parasitism rates. We treated parasitoids with similar cocoon morphology as single taxonomic units. Because some of these units may contain several morphologically similar parasitoid species (Vindstad et al. 2010), we hereafter use the term parasitoid ‘species group’ as a substitute for parasitoid ‘species’ when referring to parasitoids that were reared in this study. A summary of the biological and taxonomic

characteristics of the encountered parasitoid groups is provided in Table 2.

In order to map the species-composition of the larval parasitoid guilds attacking the three focal geometrids in the study region, we first calculated the total number of larvae parasitized throughout the study period for each combination of geometrid species \times parasitoid species group \times location. Subsequently, we calculated the number of parasitoid species groups reared from each geometrid species within and across all locations. For each geometrid species, parasitoid groups that had been recorded from less than five larvae throughout the whole study period were considered likely to represent mistakes during lab work. Such groups were, therefore, excluded from the data.

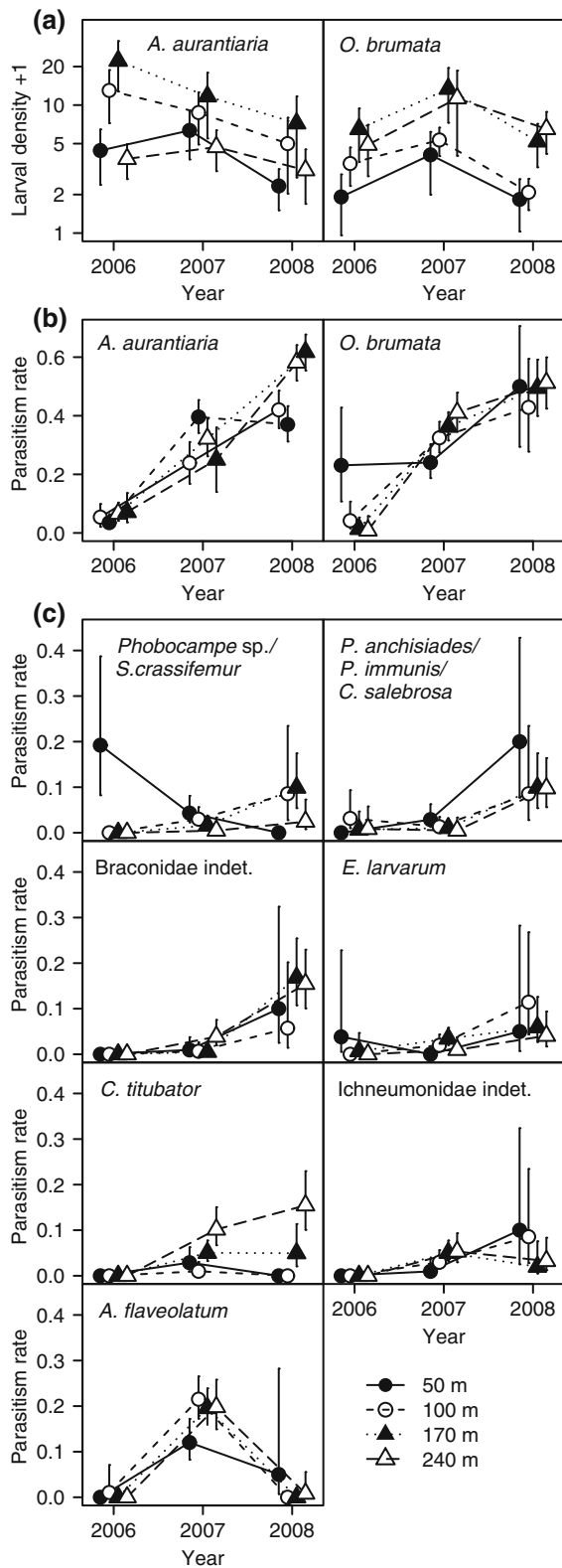


Fig. 2 Estimated densities and parasitism rates of *O. brumata* and *A. aurantiaria* larvae in the altitudinal gradient at Storelva during 2006–2008. **a** Mean larval densities on logarithmic scale (with a constant value of one added to avoid zero values) of both geometrid species for each year and altitude. **b** Total larval parasitism rates of both geometrid species for each year and altitude (representing exclusively the parasitoid group *Phobocampe* sp./*S. crassifemur* in the case of *A. aurantiaria*). **c** Larval parasitism rates of *O. brumata* by individual parasitoid species groups for each year and altitude. Error bars represent 95 % CI. The intervals for parasitism rates were obtained by fitting a separate logistic regression model, containing only an intercept, to the parasitism data for each date-altitude combination, and subsequently back-transforming the confidence interval for the intercept in each model from logit- to proportion-scale

Species-composition and prevalence of larval parasitoid guilds in the native ranges of invasive geometrids

We obtained information about the larval parasitoid guilds attacking *O. brumata* and *A. aurantiaria* in their native ranges by surveying the published literature on larval parasitism of these geometrids in Western Europe (including Britain and southern Sweden). The relevant studies for *O. brumata* were Wylie (1960), Herting (1965), Hassell (1966), Sechser (1970), Varley et al. (1973) and Vansan and Spitzer (1993), collectively covering 9 different European countries (Table 3) and a wide range of broadleaved larval host trees [including beech (*Fagus* sp.), birch (*Betula* sp.), hazel (*Corylus* sp.), oak (*Quercus* sp.) and various fruit trees]. The only relevant study for *A. aurantiaria* was Kenis et al. (2005), dealing with parasitism of both *A. aurantiaria* and *E. autumnata* on European larch (*Larix decidua* Mill.) in Switzerland. We included the results for both geometrids in our survey, to help assess whether these two species have comparable larval parasitoid guilds under native conditions. Results from the literature survey were grouped according to country, which was the finest level of spatial resolution available for all surveyed studies. As a measure of sampling effort, we recorded the total number of larvae sampled and the total number of sampling locations used, within each country, across all surveyed studies. For some countries, one or more authors had not specified sample sizes or the exact number of sampling locations used. For these countries, we report the number of larvae which we know to have been sampled and the minimum number of sampling locations which may have been used. Sampling efforts for *O. brumata* in the

Table 1 Number of *E. autumnata*, *O. brumata* and *A. aurantiaria* larvae found to be parasitized by each parasitoid species group throughout the study period at each of the locations Lyngen (Lyng), Skogsfjord (Skog), Storelva (Stor) and Reinøya (Rein)

Host species	<i>E. autumnata</i>			<i>O. brumata</i>				<i>A. aurantiaria</i>	
	Lyng	Skog	Rein	Lyng	Skog	Stor	Rein	Skog	Stor
<i>Parasitoid family and species group</i>									
<i>Ichneumonidae</i>									
<i>Agrypon flaveolatum</i>	1	–	123	217	1	208	1,100	–	–
<i>Cryptus titubator</i>	3	–	7	91	11	74	474	–	–
<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i>	15	–	248	200	97	46	2,016	40	753
<i>Ichneumonidae</i> indet.	–	–	–	–	68	52	90	–	–
<i>Braconidae</i>									
<i>Aleiodes gastritor</i>	28	–	82	–	–	–	–	–	–
<i>Protapanteles anchisiades</i> / <i>P. immunis</i> / <i>Cotesia salebrosa</i>	1	1	17	28	50	49	313	–	–
<i>Zele deceptor</i>	38	3	362	–	–	–	–	–	–
<i>Braconidae</i> indet.	–	–	–	2	82	54	106	–	–
<i>Eulophidae</i>									
<i>Eulophus larvarum</i>	14	4	70	52	26	39	153	–	–
# species groups	7	3	7	6	7	7	7	1	1
Total # species groups	7			7				1	
n	242	196	7,333	1,735	2,560	1,970	11,974	247	3,509
# years	1	2	7	2	1	3	7	1	4

Also shown is the number of parasitoid species groups reared from each geometrid species throughout the study period, within and across all locations. “n” and “# years” refer to the number of larvae sampled and the number of years of sampling, respectively, for each geometrid species at each location. Zero values were replaced with a minus symbol to improve the readability of the table

Table 2 Taxonomic and biological characteristics of the individual parasitoid species groups encountered in this study

Parasitoid family and species group	Eclosion	Development in/on host
<i>Ichneumonidae</i>		
<i>Agrypon flaveolatum</i> (Grav.)	Late	Solitary endoparasitoid
<i>Cryptus titubator</i> (Thunb.)	Late	Solitary endoparasitoid
<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i> (Thoms.)	Early	Solitary endoparasitoid
<i>Ichneumonidae</i> indet.	Late	Solitary endoparasitoid
<i>Braconidae</i>		
<i>Aleiodes gastritor</i> (Thunb.)	Early	Solitary endoparasitoid
<i>Protapanteles anchisiades</i> (Nix.)/ <i>P. immunis</i> (Hal.)/ <i>Cotesia salebrosa</i> (Marsh.) ^a	Early	Solitary endoparasitoid
<i>Zele deceptor</i> (Wesm.)	Early ^c	Solitary endoparasitoid
<i>Braconidae</i> indet. ^b	Early	Gregarious endoparasitoid
<i>Eulophidae</i>		
<i>Eulophus larvarum</i> (L.)	Early	Gregarious ectoparasitoid

Early-eclosing groups emerge from host larvae, while late-eclosing groups emerge from host pupae

^a Genetic analyses suggest that this parasitoid group probably includes at least two different parasitoid species (Vindstad et al., unpublished data)

^b Corresponds to ‘yellow cluster’ in Vindstad et al. (2010)

^c Ecloses from host larvae that have ceased feeding and are preparing for pupation

Table 3 Larval parasitoid species and total larval parasitism rates reported from *O. brumata* feeding on various host plants across north-western Europe

Host plant	Broadleaved trees					<i>V. myrtillus</i> , Broadleaved trees		Incidence
	Southern Sweden	Britain	Netherlands, Belgium	Germany	France	Switzerland	Former Czechoslovakia ^a	
Country	a, d	a, c, e	a	a, b, d	a, d	a, d	d, f	
References								
<i>Parasitoid family and species</i>								
Ichneumonidae								
<i>Agrypon flaveolatum</i> (Grav.)	×	×	×	×	×	×	×	0.55
<i>Lissonota biguttata</i> (Holmg.)	–	×	×	×	×	–	–	0.19
<i>Netelia latungula</i> (Thoms.)	×	–	×	×	–	×	–	0.28
<i>Phobocampe crassiuscula</i> (Grav.)	×	×	–	×	×	×	×	0.40
<i>Sinophorus turionum</i> (Ratzbg.)	–	–	×	×	×	–	–	0.11
Braconidae								
<i>Cotesia Jucunda</i> (Marsh.)	–	–	–	×	×	×	×	0.26
<i>Meteorus</i> sp. ^b	–	–	–	×	–	–	–	0.06
<i>Rogas luteus</i> (Nees)	×	–	–	–	×	–	–	0.09
Tachinidae								
<i>Blondelia nigripes</i> (Fall.)	–	–	–	×	–	–	–	0.09
<i>Cyzenis albicans</i> (Fall.)	×	×	×	×	×	×	×	0.83
<i>Lypha dubia</i> (Fall.)	×	×	×	×	×	×	×	0.51
<i>Panzeria laevigata</i> (Mg.)	–	×	–	×	–	–	–	0.04
<i>Phorocera obscura</i> (Fall.)	×	×	×	×	×	×	×	0.47
<i>Phryxe magnicornis</i> (Zetterst.)	–	–	–	×	×	–	–	0.11
<i>Phryxe nemea</i> (Mg.)	–	–	–	–	×	–	–	0.04
<i>Smidtia conspersa</i> (Mg.)	–	–	–	×	–	–	–	0.09
<i>Zenillia libatrix</i> (Panz.)	–	–	–	×	–	–	–	0.06
Eulophidae								
<i>Eulophus larvarum</i> (L.)	×	–	–	×	×	–	–	0.21
# species	8	7	7	16	16	12	6	Tot. # species = 18

Table 3 continued

Host plant	Broadleaved trees						V. myrtilus, Broadleaved trees Former Czechoslovakia ^a	V. myrtilus Austria	Incidence
	Southern Sweden	Britain	Netherlands, Belgium	Germany	France	Switzerland			
Country	a, d	a, c, e	a	a, b, d	a, d	a, d	d, f	d	
References									
Range total parasitism	–	Usually <0.30	–	0.04–0.60	–	–	<0.01–0.28	–	
Median total parasitism	–	–	–	0.49	–	–	0.02	–	
n (n parasitism rates)	64,249	>3,740 (?)	5,544	>73,360 (498)	97,078	18,333	19,108 (6,408)	28,205	$\Sigma n = >30,9617$
# locations	4	1	7	21	≥ 4	≥ 3	≥ 6	≥ 1	Σ locations = ≥ 47

× denotes presence of a species and – denotes absence. “n” and “# locations” refer to the number of larvae sampled and the number of sampling locations used per country, respectively. When n is reported to be greater than (>) a given number, the full sample size is unknown and the given value is the number of larvae we know to have been sampled. When # locations is reported to be greater than, or equal to (\geq), a given number, the true number of locations is unknown and the given value is the minimum number of locations which may have been used. Incidence refers to the number of sampling locations where a given parasitoid species has been recorded, out of the total number of locations used across all studies. *References*: a = Wylie (1960), b = Herting (1965), c = Hassell (1966), d = Sechser (1970), e = Varley et al. (1973), f = Vansan and Spitzer (1993)

^a It is not known whether the sampling locations of Sechser (1970) were located within the present-day Czech Republic or Slovakia

^b *Meteorus* sp. was recorded both by Wylie (1960) and Sechser (1970). It is unclear if these recordings represent the same parasitoid species

Netherlands and Belgium were relatively small, and data from these two neighbouring countries were, therefore, pooled for this geometrid species.

For each country, we recorded the number and identity of larval parasitoid species reported from the respective hosts, across all surveyed studies. We also recorded estimates of total larval parasitism rates (i.e., summed parasitism rates across all parasitoid species) when these were available. We sought to compile conservative species lists, excluding parasitoids which seemed likely to have been reported because of mistakes or confusion about identity. Therefore, we excluded parasitoid species which had not been reared in any of the studies we surveyed, but which some of the authors reported to have been encountered in earlier investigations within their study region. We also excluded parasitoids which had not been identified beyond the family level and which were ambiguous as to the number of species they represented [relevant only for about ten specimens in Kenis et al. (2005)]. Finally, we excluded five parasitoid species which Wylie (1960) reported to have reared from a single *O. brumata* larva each, but which had not been recorded in any of the other studies. Several authors dealing with *O. brumata* failed to report the prevalence of some or all parasitoid species in their data, thereby making it impossible to exclude very rare (i.e., uncertain) parasitoids. Therefore, our species lists for this geometrid may still contain some spurious recordings.

As an alternative measure of the occurrence of individual parasitoid species in *O. brumata*, we calculated the proportion of sampling locations where each individual species had been recorded, out of the total number of locations used across all surveyed studies (hereafter referred to as ‘incidence’). Calculations were based on the minimum number of locations that may have been used and the minimum number of locations where each species may have been recorded. We did not exclude parasitoid species based on their incidence, but it seems likely that species with very low incidence scores can be regarded as potentially spurious recordings. Calculation of incidence for parasitoids of *A. aurantiaria* and *E. autumnata* was not considered meaningful, owing to the relatively small number of sampling locations used for these two geometrids (see “Results”).

All parasitoid species names from the studies we surveyed were checked against the online databases

“Fauna Europaea” (Fauna Europaea 2011), “Home of Ichneumonidea” (<http://www.taxapad.com/>) and “Systema Dipteroorum” (Pape and Thompson 2010) and updated if the originally given names were no longer valid. Parasitoid names which were updated in this way are listed in Appendix 1 (ESM).

Statistical analysis

We used logistic regressions to analyse larval parasitism rates of *O. brumata* and *A. aurantiaria* at Storelva during 2006–2008. None of the individual parasitoid groups of *O. brumata* were prevalent enough to be analysed separately and *A. aurantiaria* was exclusively attacked by a single parasitoid group. Therefore, regressions were only conducted for total parasitism. In order to compare total parasitism between the two geometrids, we regressed total parasitism rates of *A. aurantiaria* on logit-transformed total parasitism rates of *O. brumata* (implying that similar parasitism rates in the two species would result in intercept = 0 and slope = 1). To ensure robust results and avoid problems with many instances of zero parasitism rates at individual sampling stations in 2006, the regression was based on year- and altitude-specific parasitism rates (i.e., parasitism samples were pooled across the sampling stations within each year-altitude combination). We also investigated if the total larval parasitism rates of the two geometrids were related to their densities. This was done by regressing the year- and altitude-specific total parasitism rates of both geometrids on their respective, log-transformed, year- and altitude-specific larval densities (i.e., mean larval densities across the sampling stations within each year-altitude combination). Because some parasitoid groups were shared between the two geometrids, such regressions were also conducted using the pooled larval densities of both species as the predictor variable. Due to the limited number of years in the dataset, there was only enough data to regress parasitism rates on current-year larval densities [i.e., parasitism (t) ~ density (t)]. Thus, we were only testing for a spatial response of parasitoids to host densities. In all regressions, quasi-likelihood methodology was implemented to correct for significant overdispersion ($p < 0.001$ in all cases for goodness-of-fit tests based on sums of squared Pearson residuals). All parameter estimates are presented with 95 % CI as a measure of uncertainty. The analyses were conducted in R 2.15.0 (R development core team 2011).

Results

Species-composition of larval parasitoid guilds in the study region

A total of 7,823 *E. autumnata* larvae, 18,239 *O. brumata* larvae and 3,756 *A. aurantiaria* larvae were sampled throughout the study period. Location-specific sample sizes are given in Table 1. Across all our sampling locations, we reared a total of seven parasitoid groups from *E. autumnata*, seven parasitoid groups from *O. brumata* and one parasitoid group from *A. aurantiaria* (Table 1; Fig. 1). One of these groups (the ichneumonid *Phobocampe* sp./*Sinophorus crassifemur*) was shared between all three geometrids, while five groups were shared between *O. brumata* and *E. autumnata*. Both *O. brumata* and *E. autumnata* also hosted two groups that were not reared from any other host species, while no such groups were found in *A. aurantiaria*. The taxonomic composition of the larval parasitoid guilds of *E. autumnata* and *O. brumata* was quite similar, with *E. autumnata* hosting three ichneumonids, three braconids and one eulophid, and *O. brumata* hosting four ichneumonids, two braconids and one eulophid. Note that all of the parasitoid groups we recorded are koinobionts [i.e., allowing the host to function normally after parasitism (Askew and Shaw 1986)].

Within each geometrid species, most of the encountered parasitoid groups were recorded at all locations where larvae had been sampled (Table 1). The only exceptions were the absence of Ichneumonidae indet. from *O. brumata* at Lyngen and the rearing of only three parasitoid groups from *E. autumnata* at Skogsfjord [the latter may have been due to small sample size and the fact that sampling occurred during the early increase phase of the moth population cycle, when parasitism is typically very low (Klemola et al. 2008, 2010)]. Although most parasitoid groups occurred at all sampling locations, the relative prevalence of individual groups varied considerably between locations (Table 1; Fig. 1).

Comparison of larval parasitism rates between *O. brumata* and *A. aurantiaria* in the study region

Operophtera brumata was parasitized by all of its seven parasitoid groups at Storelva (Table 1). In general, the prevalence patterns of these groups were

rather well synchronized across altitudes and years (Fig. 2c). All groups (except *Phobocampe* sp./*S. crassifemur* at 50 m) showed very low prevalence or absence at all altitudes in 2006. Prevalence generally remained low or increased somewhat to 2007, depending on species group and altitude. This was followed by a further increase in prevalence to 2008 across most groups and altitudes. The only group that deviated from this pattern was *Agrypon flaveolatum*. It was very rare or absent at all altitudes in 2006 and 2008, but was the most prevalent group along the entire altitudinal gradient in 2007. The group-specific prevalence patterns resulted in a very low total parasitism rate of *O. brumata* at all altitudes (except 50 m) in 2006 (Fig. 2b). Total parasitism then increased across all altitudes from 2006 to 2007 and again from 2007 to 2008.

Parasitism of *A. aurantiaria* at Storelva was exclusively accounted for by *Phobocampe* sp./*S. crassifemur* (Table 1). Despite this, total parasitism rates of *A. aurantiaria* were remarkably similar to those of *O. brumata* across altitudes and years [Figs. 2b, 3. Logistic regression of total parasitism of *A. aurantiaria* on logit-transformed total parasitism of *O. brumata* (year- and altitude-specific parasitism estimates); intercept = $-0.07 (\pm 0.37)$, slope = $0.81 (\pm 0.36)$, $p = 0.001$, $df = 10$]. There were no clear altitudinal patterns in the total parasitism rates of *O. brumata* or *A. aurantiaria* in any of the study years.

Densities of *O. brumata* were highest at 170 and 240 m and reached a peak at all altitudes in 2007 (Fig. 2a). *A. aurantiaria* was most abundant at 100 and 170 m and peaked at these altitudes in 2006, followed by a gradual decline throughout 2007 and 2008. At 50 and 240 m, densities of *A. aurantiaria* peaked in 2007 (Fig. 2a). None of the geometrids showed evidence for a relationship between their own current-year larval density and their total parasitism rates [logistic regression of total parasitism on current-year log-transformed larval density (year- and altitude-specific estimates); *O. brumata*: intercept = $-1.47 (\pm 1.40)$, slope = $0.35 (\pm 0.75)$, $p = 0.37$, $df = 10$. *A. aurantiaria*: intercept = $0.23 (\pm 1.23)$, slope = $-0.63 (\pm 0.70)$, $p = 0.10$, $df = 10$]. Similarly, there was no evidence for a relationship between current-year pooled larval density and total parasitism in either geometrid species [logistic regression of total parasitism on current-year log-transformed pooled larval density (year- and altitude-specific estimates);

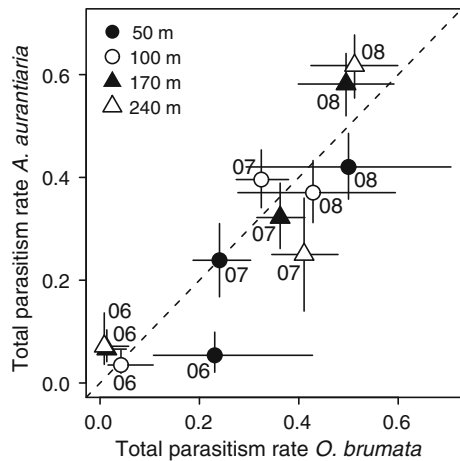


Fig. 3 Scatter plot displaying the co-variation between estimated total larval parasitism rates of *O. brumata* and *A. aurantiaria* across years and altitudes in the altitudinal gradient at Storelva. 06 = 2006. 07 = 2007. 08 = 2008. Error bars represent 95 % CI. The intervals were obtained by fitting a separate logistic regression model, containing only an intercept, to the parasitism data for each date-altitude combination, and subsequently back-transforming the confidence interval for the intercept in each model from logit- to proportion-scale

O. brumata: intercept = -0.40 (± 2.40), slope = -0.19 (± 0.93), $p = 0.70$, $df = 10$. *A. aurantiaria*: intercept = 0.13 (± 1.87), slope = -0.43 (± 0.82), $p = 0.32$, $df = 10$].

Species-composition and prevalence of larval parasitoid guilds in the native ranges of invasive geometrids

The studies we surveyed for *O. brumata* had a collective sample size of more than 300,000 larvae, sampled from at least 47 different locations. The number of larvae and locations sampled per country are given in Table 3. A total of 18 different larval parasitoid species reported by these studies entered our species list, including five ichneumonids, three braconids, nine tachinids and one eulophid (Table 3). Only five of these species appeared to have been regularly encountered, being reported from all studied countries (except for the absence of *Phobocampe crassiuscula* in the Netherlands/Belgium) and showing an incidence of more than 0.40. Of the remaining 13 species, six had been encountered more or less sporadically, being reported from three to six countries and showing an incidence of between 0.10 and ≈ 0.30 , while seven had been encountered very rarely, being

reported from only one to three countries and showing an incidence of less than 0.10. The countries with the highest number of parasitoid species were Germany and France, both with 16 species. The number of parasitoid species encountered in the remaining countries ranged between six and twelve.

Herting (1965), studied *O. brumata* on various broadleaved tree species at Westfalen, Germany, and estimated total larval parasitism rates of 0.04–0.60 (median = 0.49) across the years 1959–1961. These estimates were based on a total of 498 larvae, sampled on just a few individual trees. The phenological stage of the larvae at the time of sampling was not reported. Varley et al. (1973) monitored larval parasitism of *O. brumata* on five individual oak trees at Wytham wood, England, throughout the years 1950–1968, and reported that total larval parasitism rates rarely rose above 0.30 throughout this period. This estimate was based on larvae which were dropping to the ground to pupate and, therefore, did not include parasitoids which eclose before the pupal drop. Larval sample sizes were not reported. Vansan and Spitzer (1993) studied parasitism of *O. brumata* on various broadleaved trees and bilberry (*Vaccinium myrtillus*) at four locations in South Bohemia, Czech Republic, during 1991–1992. They reported that total larval parasitism rates varied from less than 0.01 to 0.28 (median = 0.02) across all locations and years, based on a total sample size of 6,408 larvae collected during the fourth and fifth instar.

The sample sizes of Kenis et al. (2005) were a total of 6,258 *A. aurantiaria* larva and 2,498 *E. autumnata* larvae, sampled from seven and ten different locations, respectively. Ten different larval parasitoid species were reared from *A. aurantiaria*, including five ichneumonids, four braconids and one tachinid (Table 4). The larval parasitoid guild of *E. autumnata* showed a similar taxonomic composition, containing a total of nine different species, including five ichneumonids, three braconids and one tachinid (Table 4). Notably though, Kenis et al. (2005) reported that ichneumonids accounted for most of the parasitism in *A. aurantiaria* while braconids were most prevalent in *E. autumnata*. Across all sites and years (1991–1994) of the study, total larval parasitism rates of 0.04–0.76 (median = 0.25) and 0–0.48 (median = 0.11) were recorded for *E. autumnata* and *A. aurantiaria*, respectively. Larvae were mostly sampled during the later instars.

Table 4 Larval parasitoid species and total larval parasitism rates reported by Kenis et al. (2005) from *E. autumnata* and *A. aurantiaria* feeding on larch in Switzerland

Host species	<i>E. autumnata</i>	<i>A. aurantiaria</i>
Host plant	<i>Larix decidua</i>	<i>Larix decidua</i>
Country	Switzerland	Switzerland
Reference	Kenis et al. (2005)	Kenis et al. (2005)
Parasitoid family	Parasitoid species	Parasitoid species
Ichneumonidae	<i>Agrypon flaveolatum</i> (Grav.)	<i>Casinaria</i> sp. ^a
	<i>Campoletis varians</i> (Thoms.)	<i>Dusona contumax</i> (Först.)
	<i>Casinaria</i> sp. ^a	<i>Ophion minutus</i> (Kriechb.)
	<i>Netelia virgata</i> (Geoffroy)	<i>Phobocampe crassiuscula</i> (Grav.)
	<i>Phobocampe</i> sp. ^b	<i>Phobocampe</i> sp. ^b
Braconidae	<i>Aleiodes gastritor</i> (Thunb.)	<i>Cotesia praepotens</i> (Hal.)
	<i>Cotesia salebrosa</i> (Marsh.)	<i>Homolobus discolor</i> (Wesm.)
	<i>Protapanteles anchisiades</i> (Nix.)	<i>Homolobus infumator</i> (Lyle)
Tachinidae	Tachinidae indet.	<i>Phryxe magnicornis</i> (Zetterst.)
# species	9	10
Range total parasitism	0.04–0.76	0–0.48
Median total parasitism	0.25	0.11
n	2,498	6,258
# locations	10	7

“n” and “# locations” refer to the number of larvae sampled and the number of sampling locations used, respectively

^{a,b} Same parasitoid species in both *A. aurantiaria* and *E. autumnata*

Discussion

The geometrids *O. brumata* and *A. aurantiaria* expanded their ranges into the coastal mountain birch forest of northern Norway roughly a century and 15 years ago, respectively. To understand the accumulation of larval parasitoids on these invaders, we compared their larval parasitoid guilds in northern Norway with the guild of the native geometrid *E. autumnata* and with the literature on their parasitoid guilds in their native ranges in Western Europe. For all three geometrids, we mostly found the same parasitoid species groups at all our sampling locations, suggesting that all important larval parasitoids in our study region were detected. *O. brumata* and *E. autumnata* both hosted seven parasitoid groups, while *A. aurantiaria* hosted only one. Assuming that parasitoid species richness of the invaders is converging towards the level of *E. autumnata*, this suggests that parasitoid accumulation in our study region has barely begun for

A. aurantiaria but is complete for *O. brumata*. Our survey of parasitism studies from Western Europe clearly supports this conclusion for *A. aurantiaria*. Kenis et al. (2005) found that sympatric native populations of *A. aurantiaria* and *E. autumnata* in Switzerland hosted similar numbers of larval parasitoid species with a similar distribution among parasitoid families. This suggests that the larval parasitoid guild of *A. aurantiaria* in our study region will become as species rich as that of *E. autumnata* over time.

The assumption of inherently similar larval parasitoid guilds in *O. brumata* and *E. autumnata* is harder to verify. At least 18 different larval parasitoid species have been recorded from *O. brumata* across Western Europe, while Kenis et al. (2005) reported only nine species from *E. autumnata* in Switzerland. However, many parasitoids of *O. brumata* showed low incidence, meaning that they may represent rare species or incidental attacks, detected because of the massive sample sizes of the studies we surveyed for this

geometrid. Alternatively, they may be spurious recordings. The countries with the largest larval samples (Germany and France) also had the most parasitoid species (16 species for both countries), supporting an effect of sample size. The other countries had six to twelve species (typically seven to nine), i.e., roughly the number that Kenis et al. (2005) found for *E. autumnata* in Switzerland. Thus, if rare or incidental parasitoids are excluded, *O. brumata* and *E. autumnata* may host about the same number of larval parasitoid species in Western Europe. However, the contrasting sampling efforts of the studies of these two geometrids make comparisons difficult.

Another complication for *O. brumata* is that half of its larval parasitoid species in Western Europe are tachinids, while this parasitoid family was absent from our samples in northern Norway. This could imply that *O. brumata* will eventually start to accumulate tachinids in our study region. However, we see no reason why *O. brumata* should accumulate tachinids slower than parasitoid wasps, which currently constitute the larval parasitoid guild of this geometrid in our study region. It might be that parasitoid wasps fulfil the same ecological role in the mountain birch system as tachinids do in Western Europe, e.g., because sub-arctic conditions do not favour tachinids.

The uncertainties outlined above for *O. brumata* mean that caution is needed when discussing how rapidly invasive geometrids accumulate larval parasitoids in our study region. Since the parasitoid guild of *A. aurantiaria* is strongly impoverished roughly 15 years after the invasion, the accumulation process probably takes at least a few decades to reach completion. If we assume that parasitoid accumulation on *O. brumata* is complete, the upper time limit for the process falls at roughly a century (i.e., the approximate residence time of *O. brumata* in the study region). This would be consistent with several reports of high (but seemingly incomplete) parasitoid accumulation on invasive hosts within a few decades of the invasion (Cornell and Hawkins 1993; Hawkins and Cornell 1994; Vercher et al. 2005; Gröbler and Lewis 2008; Grabenweger et al. 2010; Folcher et al. 2011). However, there is also evidence that the accumulation is sometimes considerably faster [i.e., <10 years (Godfray et al. 1995)] or slower [i.e., >150 years (Cornell and Hawkins 1993; Hawkins and Cornell 1994; Schönrogge et al. 1995)]. The latter may

apply to our system if parasitoid accumulation on *O. brumata* is still incomplete.

At least three mechanisms can explain gradual accumulation of parasitoids on invasive hosts. First, native parasitoids may gradually adapt (behaviorally, physiologically or phenologically) to invasive hosts (Cornell and Hawkins 1993; Hawkins and Cornell 1994; Grabenweger et al. 2010). It may be easy for parasitoids of the native *E. autumnata* to adapt to related invasive geometrids like *O. brumata* and *A. aurantiaria*, and the sharing of several parasitoid groups between the three geometrids makes it seem likely that the invaders have acquired parasitoids from *E. autumnata*. If this is true, our inferences about parasitoid accumulation rates may apply only to systems where a native relative acts as a source of parasitoids for invasive hosts. A related point is that parasitoid accumulation in our study region may be faster in *O. brumata* than in *A. aurantiaria*, since *O. brumata* is more closely related to *E. autumnata* than *A. aurantiaria* is (*E. autumnata* and *O. brumata* belong to the subfamily Larentiinae, while *A. aurantiaria* belongs to the subfamily Ennominae). Second, as invasive hosts spread throughout new habitat types in their invaded ranges, they may gradually encounter and accumulate more parasitoid species (Cornell and Hawkins 1993; Hawkins and Cornell 1994; Grabenweger et al. 2010). However, this mechanism seems implausible for our system. Although *A. aurantiaria* occurs throughout the study region (Jepsen et al. 2011) and has probably spread into most of the habitat types in the coastal mountain birch system, it has so far accumulated just one parasitoid species group. Third, if a host expands its range by gradual geographical spread (as is the case for the studied invasive geometrids), parasitoids from the native range may fall behind the invasion front but eventually pursue the host into the invaded range (Gray et al. 2008; Tobin et al. 2009). The mobility of the studied geometrids and parasitoids is poorly known, but there is evidence that first-instar geometrid larvae may disperse several kilometers by ballooning (Leggett et al. 2011). Thus, these geometrids may be able to escape from their parasitoids during range expansion. Several of the parasitoids we reared from *O. brumata* and *A. aurantiaria* also occur in Western Europe. However, we also reared all of these parasitoids from *E. autumnata*. Thus, they may have pursued the invasive geometrids into the study region,

but the invaders may also have recruited them locally after the invasion. A phylogeographic study could reveal the origin of the parasitoids attacking *O. brumata* and *A. aurantiaria* in our study region (Hayward and Stone 2006; Nicholls et al. 2010).

Similarly to parasitoid species richness, total parasitism rates of invasive hosts tend to increase with their residence times in invaded areas (Schönrogge et al. 1998; Gröbler and Lewis 2008; Menéndez et al. 2008). However, we found that total larval parasitism rates of *O. brumata* and *A. aurantiaria* at Storelva were closely matched across both years and altitudes. Correspondingly, Schott et al. (2012) reported similar total larval parasitism rates in *E. autumnata* and *O. brumata* at Reinøya. Thus, somewhat surprisingly, the three studied geometrids seem to suffer similar levels of larval parasitism, despite contrasting residence times in the study region. This finding sheds light on three important aspects:

First, our results suggest that the establishment and spread of invasive geometrids in coastal mountain birch forest is not facilitated by release from larval parasitoids. *A. aurantiaria* seems to suffer just as much from larval parasitism as the long established *O. brumata* and the native *E. autumnata*, but has still managed to rapidly invade the study region and reach outbreak densities locally (Jepsen et al. 2011). The literature on parasitism in Western Europe also argues against a parasitoid release for *A. aurantiaria* in our system. Kenis et al. (2005) typically found somewhat lower larval parasitism in native *A. aurantiaria* populations in Switzerland than in sympatric *E. autumnata* populations. Thus, the similar parasitism rates of the two geometrids in our study region clearly suggest that *A. aurantiaria* does not experience reduced parasitism in the mountain birch system due to its status as an invader. Moreover, the parasitism rates reported for *A. aurantiaria* in Switzerland are very similar to those in our study region, again arguing against a parasitoid release. The parasitism data for *O. brumata* from Western Europe yields similar conclusions. Nothing in these data suggests that *O. brumata* normally suffers higher parasitism than *E. autumnata*, or has higher parasitism in its native range than in our study region. However, most of the studies reporting parasitism rates for *O. brumata* were conducted on small spatial scale and failed to report sample sizes or larval phenology at sampling. Thus, their results should be interpreted cautiously. Also,

O. brumata may have experienced parasitoid release in our study region shortly after its invasion, without this effect being observable a century later. Thereby, our inferences about a lack of parasitoid release in invasive geometrids are most robust for *A. aurantiaria*. The conclusion that geometrid invasions in coastal mountain birch forest are probably not facilitated by larval parasitoid release corresponds with recent findings of Hagen et al. (2010) and Schott et al. (2010), namely that geometrid population cycles in this system are unlikely to be driven by larval parasitoids.

Second, our results indicate that there is no relationship between diversity and overall functionality (i.e., mortality inflicted on host populations) in the studied larval parasitoid guilds. The single parasitoid group of *A. aurantiaria* can apparently inflict similar overall mortality as the seven groups of *E. autumnata* and *O. brumata*. To explain similar results from another system, Rodríguez and Hawkins (2000) suggested that the resource-utilization modes of many parasitoids are too similar to be complementary (but see Tylianakis et al. 2006). This explanation seems highly plausible for our results with a single type of parasitoid guild, where species may exploit host resources in largely similar ways. Our results also support earlier suggestions by Vindstad et al. (2010, 2011), namely that total larval parasitism rates of birch forest geometrids may be largely independent of the identity and diversity of attacking parasitoid species.

Third, the observed spatiotemporal matching between the parasitism rates of *A. aurantiaria* and *O. brumata* suggests that some unknown factor is synchronizing total larval parasitism of different geometrid species in the study region, both across different years and environmental contexts (i.e., altitudes). Since *A. aurantiaria* and *O. brumata* hosted contrasting numbers of parasitoid species groups, parasitoid diversity is clearly not important in this respect. It also seems that parasitism is not governed by host density. Larval densities of *A. aurantiaria* and *O. brumata* at Storelva contrasted across years and altitudes, but without corresponding differences in total parasitism rates. Also, we found no evidence for a spatial response of parasitoids to species-specific or pooled current-year larval density. However, it seems likely that larval parasitism of birch forest geometrids may somehow be governed by inter-annual climatic variation. Parasitoid flight activity can be sensitive to precipitation, wind and rain, and climate can also

affect phenological synchronization with hosts (Vindstad et al. 2011). Thus, climate could strongly impact total parasitism rates, across different geometrid species.

Conclusion

By comparing parasitism between the native *E. autumnata* and the invasive *O. brumata* and *A. aurantiaria*, we have found evidence that larval parasitoid guilds of invasive birch forest geometrids are severely species-impooverished shortly after the invasion, but may attain native levels of species richness within a few decades to at least a century (albeit with considerable uncertainty for the upper time limit). We found no corresponding temporal pattern in total larval parasitism rates, suggesting that invasive geometrids in the study region do not enjoy release from larval parasitism, despite delays in parasitoid accumulation. In support of this conclusion, a literature survey suggests that these invaders do not suffer less from parasitism in the study region than in their native ranges. Our results also demonstrate a distinct absence of diversity-functionality relationships in the studied parasitoid guilds, and suggest that total larval parasitism rates of geometrids in the study region are governed by some common external factor which is independent of parasitoid species richness and larval density.

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