

# Sources of variation in larval parasitism of two sympatrically outbreaking birch forest defoliators

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**Abstract.** 1. Studies of insect communities rarely support the parasitoid–host regulation hypothesis. Spatio-temporal variation in parasitoid prevalence due to complex food web interactions or abiotic factors may prevent parasitoids from regulating hosts.

2. We examined the relative contribution of spatial (altitude) and temporal (years) sources to total variation in parasitoid prevalence rates in outbreaks of *Epirrita autumnata* Borkhausen and *Operophtera brumata* Linnaeus populations. We tested whether prevalence rates of generalist parasitoids were correlated between sympatric host populations and to what extent any of the parasitoids were host density dependent.

3. Four larval parasitoids (two specialists and two generalists) exhibited significantly structured spatio-temporal dynamics over years and altitudes. The prevalence rates of one of the generalists were spatio-temporally correlated between the two host species, while for the other they were not.

4. Three parasitoids showed tendencies for direct or delayed positive density dependence as expected from numerical and functional responses to their hosts. However, the effects were weak and minute compared to the variation attributed to year and altitude.

5. We conclude that unknown aspects of the larval parasitoid ecology that co-vary with altitude and year in the study system dominate their prevalence dynamics and thus act to hinder density-dependent responses that could potentially regulate host populations.

**Key words.** Altitude, gradient, insect outbreak, natural enemies, population cycles, predation, weather.

## Introduction

Parasitoids have often been suggested to cause complex temporal dynamics in host populations, such as cycles (Berryman, 2002). However, so far few researchers have demonstrated the capability of parasitoids to regulate insect hosts in natural settings. Studies providing support for parasitoid regulation have been derived from biological control programmes, in which exotic parasitoids were applied to depress (mainly exotic) economical pest species (Roland & Embree, 1995; Neuenschwander, 2001; Sarfraz *et al.*, 2005). Other researchers have inferred parasitoid regulation

from mathematical modelling (Godfray & Shimada, 1999; Hassell, 2000; Tanhuanpää *et al.*, 2002; Turchin *et al.*, 2003) or small-scale field experiments (Klemola *et al.*, 2010). However, at the operative spatial and temporal scales at which host–parasite dynamics are played out in native study systems, ecologists struggle to detect the predicted regulatory role of parasitoids (Hawkins *et al.*, 1999; Rodriguez & Hawkins, 2000; Hagen *et al.*, 2010; Schott *et al.*, 2010). What causes this controversy?

One possibility is that the role of parasitoids is context dependent. That is, food web interactions (including their natural spatio-temporal scales; cf. Gripenberg & Roslin, 2007) or the abiotic environment of native systems may differ significantly from laboratory set-ups or exotic systems. Evidence for parasitoid-mediated host dynamics drawn from simplified food webs might not apply to native ecosystems (Hawkins *et al.*, 1999). Accordingly, top-down control of hosts is likely to be more common for single specialised

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parasitoid species in simplified environments (i.e. agrosystems or experimental settings) rather than with guilds of parasitoids imbedded in complex food web interactions (Montoya *et al.*, 2003; Eveleigh *et al.*, 2007) and/or being subjected to the disrupting effects of abiotic environmental variation (Bale, 1993; Bouchier & Smith, 1996; Fournier & Boivin, 2000; Gu & Dorn, 2001).

The moth species *Epirrita autumnata* Borkhausen (autumnal moth) and *Operophtera brumata* Linnaeus (winter moth) (Lepidoptera, Geometridae) are prime examples of cyclic outbreak dynamics that have been proposed to be driven by larval parasitoids (Berryman, 1996; Klemola *et al.*, 2002; Tanhuanpää *et al.*, 2002). However, the empirical evidence for this proposal is inconsistent. In the continental section of the sub-arctic birch forest in northern Fennoscandia, the cold tolerant *E. autumnata* is the dominant geometrid. This species is exhibiting cyclic population outbreaks in this region and time series data suggest that larval parasitoids exhibit the delayed density-dependent parasitism necessary to drive population cycles (Tanhuanpää *et al.*, 2002; Ims *et al.*, 2008). A recent field experiment has shown the expected release of *E. autumnata* populations in continental forest when parasitoids were eliminated by means of enclosures (Klemola *et al.*, 2010). In the coastal section of the sub-arctic birch forest, the winters are considerably milder and allow *O. brumata* to be co-dominant with *E. autumnata*. Both geometrids may exhibit population cycles similar to those seen in continental forests for *E. autumnata*, albeit with two interesting distinctions. First, in the mountainous landscape of the coastal section the outbreak cycles of both moth species appear to be most pronounced at high altitudes (i.e. close to the alpine forest line; Hagen *et al.*, 2007; Tenow *et al.*, 2007). This altitudinal pattern could be due to mismatched phenology between geometrid larvae and parasitoids close to the tree line (Van Nouhuys & Lei, 2004; Hagen *et al.*, 2007). Second, the outbreaks of *O. brumata* regularly lag 1–3 years behind the outbreaks of the sympatric *E. autumnata* (Tenow *et al.*, 2007; Hagen *et al.*, 2008, 2010; Klemola *et al.*, 2008). The lagged dynamics have been proposed to be partly caused by differential impacts of larval parasitoids on the two hosts; *E. autumnata* being the geometrid most impacted (Klemola *et al.*, 2009).

In the case of the sympatric *E. autumnata* and *O. brumata* in the coastal forests we have recently shown that larval parasitism did not affect the growth rate of moth populations during the critical peak and crash phase of the moth population cycle as would be expected from direct (first order) and delayed (second order) density dependence (Hagen *et al.*, 2010; Schott *et al.*, 2010). This was surprising, even though the larvae of both geometrid species suffer parasitoid inflicted mortality rates as high as those found in continental populations of *E. autumnata*. There may be two potential reasons for this. First, the food web in which the two geometrids are likely to function as main nodes has never been fully mapped (cf. Eveleigh *et al.*, 2007 for food web map centred on spruce budworms). Consequently, possible interactions acting compensatory to larval parasitism have not been explored (Schott *et al.*, 2010). Second, a high degree of spatial and temporal

environmental variation in the coastal birch forest system may disrupt the possibly expected host–parasitoid dynamics following from functional and numerical responses of parasitoids.

In the present paper, we investigate the dynamics of the parasitoids. Specifically, we assess the extent of spatial and temporal variation in species-specific parasitoid prevalence, which cannot be explained as responses to (or bottom-up effects of) host densities. The study was designed to encompass the typical setting of sympatric geometrid dynamics in sub-arctic coastal birch forest; i.e. an altitudinal gradient in outbreak amplitude of both geometrid species and lagged *O. brumata* dynamics relative to *E. autumnata* at high altitudes (Schott *et al.*, 2010).

## Materials and methods

### Study system

The study was carried out within a belt of continuous mature mountain birch (*Betula pubescens czerepanovii* Orlova) forest on the island Reinøya (70°00'N, 19°49'E) in the coastal district of Troms County in northern Norway. Ten replicate altitudinal transects were established. Each transect had one sampling station each at four altitudes; i.e. at 30, 100, 170, and 240 m above sea level (see also Mjaaseth *et al.*, 2005; Hagen *et al.*, 2008; Schott *et al.*, 2010). The highest altitude (240 m) is at the alpine tree line. As Edland (1971) reported wind dispersal (ballooning) of *O. brumata* larvae to be unimportant beyond a distance of 50 m, the altitudinal transects were spaced at 200-m intervals at each altitude to avoid dispersal-related dependence among the transects and sampling stations. Additionally, females of *O. brumata* are wingless and cannot disperse through the air, while females of *E. autumnata* are considered to be bad flyers due to their heavy egg load (Tammara *et al.*, 1995). Statistical independence between the sampling stations (i.e. no spatial autocorrelation) has been verified by Schott *et al.* (2010).

The most common spring feeding insect folivores on birch in the study area are *E. autumnata* and *O. brumata*. Both geometrids are univoltine with non-overlapping generations. Eggs are laid during autumn on tree trunks and twigs and hatch in spring in concert with bud burst. The solitary larvae undergo five instars during early summer. Feeding occurs mainly on mountain birch in northern Fennoscandia and lasts approximately 1–1.5 months until early July. After that, moth larvae pupate in the soil. Typically, *E. autumnata* eggs hatch before those of *O. brumata* (Jepsen *et al.*, 2011). Mjaaseth *et al.* (2005) found that in 2 years of those covered by the present study (2001–2002) that *E. autumnata* completed the larval stage approximately 10 days earlier than *O. brumata*.

In the study area, the two geometrids harbour a guild of eight identifiable larval parasitoids, one species group (the putative species *Phobocampe* sp. and *Sinophorus crassifemur* cannot at present be distinguished) and one unknown Braconidae (Table 1). Of these, only four species/species groups had prevalence high enough to warrant analyses. Two of the parasitoids were found commonly in both host species and thus in the following were termed generalists (*Phobocampe*

**Table 1.** Summary of the parasitoid groups defined in the present study.

Parasitoid species/group	Host species	Eclosion	References
<b><i>Phobocampe</i> sp.</b>	<i>E. autumnata</i> , <i>O. brumata</i>	Early	Teder <i>et al.</i> (2000)
<b><i>Sinophorus crassifemur</i> (Thompson)</b>			
<i>Protapanteles anchisiades</i> (Nixon)	<i>E. autumnata</i> , <i>O. brumata</i>	Early	Klemola <i>et al.</i> (2007) Teder <i>et al.</i> (2000) Kenis <i>et al.</i> (2005)
<i>P. immunis</i> (Haliday)			
<i>Cotesia salebrosa</i> (Marshall)			
<i>Eulophus larvarum</i> (Linnaeus)			
<b><i>Agrypon flaveolatum</i> (Gravenhorst)</b>	<i>E. autumnata</i> , <i>O. brumata</i>	Late	Kenis <i>et al.</i> (2005)
<i>Aleiodes</i> cf. <i>gastritor</i> (Thunberg)	<i>E. autumnata</i>	Early	Teder <i>et al.</i> (2000)
<b><i>Zelexceptor</i> (Wesmael)</b>	<i>E. autumnata</i>	Late	Virtanen and Neuvonen (1999)
<b><i>Cryptus titubator</i> (Thunberg)</b>	<i>O. brumata</i>	Late	
Braconidae	<i>O. brumata</i>	Early	

Only groups in bold were used in the analyses.

sp./*S. crassifemur* and *Agrypon flaveolatum*). The two other species were only found in one host each and for that reason were termed specialists (*Cryptus titubator* in *O. brumata* and *Zelexceptor* in *E. autumnata*). All parasitoid species in our study were solitary koinobionts with one generation per year. No superparasitism was recorded during the study.

#### Host density estimation and parasitoid sampling

Geometrid larval density and parasitoid prevalence at the 40 sampling stations were estimated during the years 2001–2005 in June when the larvae of both geometrid species were in the fourth to fifth instar. We used a standardised sampling methodology described in detail in Schott *et al.* (2010). Larval abundance estimation was based on counting all larvae on 10 equally sized birch branches at individual sampling stations. Collection of larvae for parasitoid rearing and assessment of parasitism was done at a radius of approximately 30 m around sampling stations until moth populations at a given altitude had concluded the crash phase of the cycle (in 2006). Densities of moth larvae never reached levels that resulted in severe defoliation of the birch forest. After the crash, adequate samples for estimation of parasitism could no longer be obtained due to scarcity of host larvae. In 2004, moths at the lowest altitude (30 m a.s.l.) had already ended their larval stage at the time of sampling and adequate samples could not be obtained. Consequently, the 30 m altitudinal transect was omitted from parts of the analysis (see below). A total of 4282 *E. autumnata* larvae and 11 832 *O. brumata* larvae were collected during the years 2001–2005. The number of larvae per year, altitude, and species used for estimation of parasitism (= prevalence) rates are given in Table 2. Larvae perishing due to unknown causes were omitted from these estimates.

Larvae were housed in 1-litre plastic boxes (8 × 15 × 8 cm) containing a soil layer for pupating and a peat moss layer for moisture maintenance. Maximally, 20 individuals (all belonging to the same sampling station) were kept in a box. We fed larvae with freshly clipped birch leaves every third day and emergence of parasitoids as well as unidentified mortality was recorded. When all larvae had either died or pupated, we

**Table 2.** Sample sizes for altitude and year of collected larvae for parasitism estimation.

Species/altitude	Year	30 m	100 m	170 m	240 m
<i>E. autumnata</i>	2001	24	92	26	60
	2002	44	80	80	184
	2003	544	909	420	861
	2004	NA	117	187	296
	2005	59	63	19	54
<i>O. brumata</i>	2001	668	674	668	337
	2002	395	849	426	315
	2003	989	497	817	805
	2004	NA	165	721	781
	2005	306	280	474	648

'NA' denotes missing data for 30 m in 2004.

stored the boxes at an outdoor location under ambient temperature conditions, sheltered from direct sunlight exposure and precipitation. Hatching was recorded in September and October. Pupae that did not hatch were dissected for detection of parasitoids.

#### Data analysis

We analysed prevalence rates of each parasitoid species (or species group) in the two hosts. The data were analysed using logistic regression models (logit-link function, binomial distribution and quasi-likelihood to correct for overdispersion; McCullagh & Nelder, 1989).

We first assessed the contribution of year (5 years) and altitude (four altitudes) to the total spatio-temporal variation in species-specific parasitoid prevalence rates among sampling stations (10 sampling stations per altitude). To obtain an orthogonal design and facilitate interpretation of results, we omitted altitude 30 m from this analysis as data for this altitude were not available for the year 2004 (see above). Hence, this analysis was conducted on 30 data points per year. We fitted logistic models with year and altitude as categorical predictors (including interaction) and assessed the adequacy of different terms by means of the model selection criterion QAICc (Akaike Information Criterion for quasi-likelihood models with

**Table 3.** Nagelkerke's  $R^2$  and QAICc for different linear combinations of the predictors (year and altitude) of parasitism rates.

Host	Model	Year		Altitude		Year + altitude		Year × altitude		Ovd.
		$R^2$	QAICc	$R^2$	QAICc	$R^2$	QAICc	$R^2$	QAICc	
<i>E. autumnata</i>	<i>Phobo./Sinoph.</i>	0.81	205	0.29	325	0.88	180	0.91	<b>171</b>	1.4
	<i>A. flaveolatum</i>	0.73	110	0.23	173	0.78	<b>103</b>	0.81	109	2.0
	<i>Z. deceptor</i>	0.88	248	0.47	412	0.93	<b>191</b>	0.94	194	1.2
<i>O. brumata</i>	<i>Phobo./Sinoph.</i>	0.91	304	0.71	396	0.98	179	0.99	<b>170</b>	1.7
	<i>A. flaveolatum</i>	0.79	225	0.6	256	0.92	182	0.95	<b>173</b>	2.7
	<i>C. titubator</i>	0.83	179	0.68	209	0.92	<b>145</b>	0.94	147	2.7

The selected models with their  $R^2$  are highlighted in grey. The overdispersion parameter (Ovd.) is given for the selected model.

a small sample correction term) (Johnson & Omland, 2004). The variation explained by the different models was assessed using Nagelkerke's  $R^2$ , which is a measure analogous to Pearson  $R^2$  but modified for generalised linear models and based on the likelihood values (Nagelkerke, 1991; Randin *et al.*, 2009).

We further assessed whether the prevalence of parasitoids exploiting both host species (i.e. the two generalists, *Phobocampe* sp./*S. crassifemur* and *A. flaveolatum*) co-varied between the two host species over time and space. As the logistic models with year and altitude as predictors (see above) accounted for most of the variation in sampling station-specific parasitoid prevalence rates (Table 3), we used logit estimates for each altitude and year (i.e. samples pooled over sampling stations for a given altitude and year). Consequently, this analysis was conducted on four altitudinal data points per year. The estimated prevalence in *E. autumnata* as response was then regressed against the prevalence in *O. brumata* as predictor.

Finally, we checked whether there was any evidence for density-dependent responses of the different parasitoids to their hosts by regressing (and plotting) the prevalence rates in year  $t$  against the logarithm of host densities in year  $t$  and  $t - 1$  and  $t - 2$ . Note that these analyses would demonstrate the bottom-up relationships expected in a strongly dependent parasite–host relationship. In addition, in these cases we used year- and altitude-specific estimates of prevalence rates (and host densities) as the response scale of the parasitoids (c.f. Results). We justify this level of aggregation of the data by the fact that population dynamics of hosts were operating at the level of different altitudes rather than separate sampling stations (see Hagen *et al.*, 2008) and that altitude and year accounted for almost all of the variation in sampling station specific data on parasitoid prevalence rates (see Results). We used linear regression analysis on unweighted logit parasitoid prevalence rates against the logarithm of host abundance (i.e. density estimates) in this case, as logistic regression models would have given higher weight to years and altitudes with high densities (i.e. binomial proportions with large denominators), which might have biased the analysis of density dependence. Whereas all 5 years could be used in the analysis of spatial density dependence ( $t$ ), the two data sets for analyses of temporal density dependence had to be restricted to prevalence rates for the years 2002–2005 (lag  $t - 1$ ) and 2003–2005 (lag  $t - 2$ ). However, from a former study (Ims *et al.*, 2004) moth density data were available

for the 170 m altitude in 1999 and 2000. These data paired with respective parasitism prevalence rates were added to the density-dependence analyses. We also included data from the 30-m altitude from these years. For the two generalist parasitoids we applied pooled host abundances (of both host species) as density predictors.

All analyses were performed in R 2.11.0 applying the functions *lm* () and *glm* (). As measures of uncertainty in parameter estimates throughout the paper, we used 95% confidence intervals.

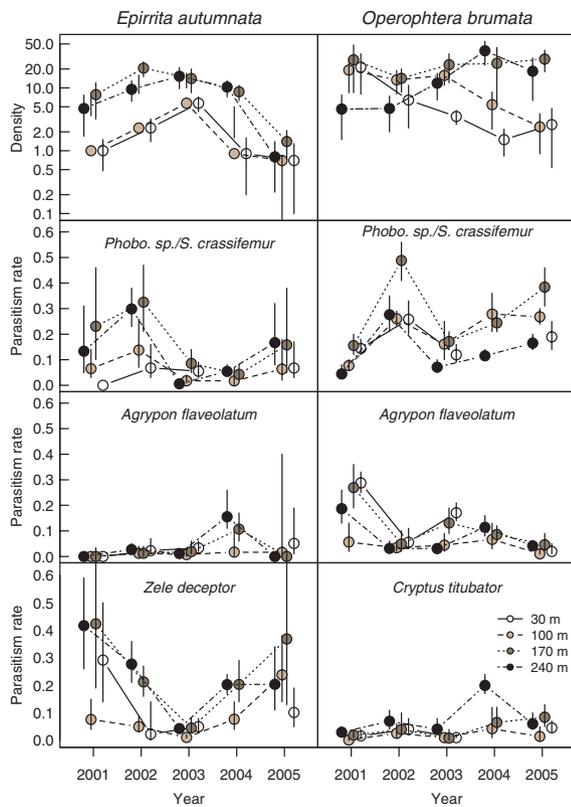
## Results

### Host dynamics

The population dynamics of geometrids in this system have been thoroughly analysed by Hagen *et al.* (2008) and Schott *et al.* (2010), and for the purpose of the present study focusing on the parasitoids we only summarise the main features of the host dynamics. Outbreaks (i.e. high peak abundances) of both hosts were most distinct at high altitudes (170 and 240 m; Fig. 1). *Operophtera brumata* also showed the typical lagged dynamics at the highest altitudes, where populations crashed after year 2005 (Schott *et al.*, 2010).

### Spatio-temporal variation in parasitoid prevalence rates

The parasitoids exhibited host-specific prevalence rates that differed significantly among years and altitudes (Fig. 1, parameters of the logistic models are provided in Tables S1 and S2). The predictors year and altitude accounted for most of the extra-binomial variation in station-specific parasitoid prevalence rates as evident from very large values of Nagelkerke's  $R^2$  with year being generally a more important variable than altitude (Table 3). In the cases of *Z. deceptor* and *A. flaveolatum* in *E. autumnata* and *C. titubator* in *O. brumata* only additive effects of year and altitude were important. In *E. autumnata*, *Z. deceptor* attained the highest prevalence rates at the two highest altitudes, but with a deep synchronous low across all altitudes in 2003 (Fig. 1). The prevalence of *A. flaveolatum* was dominated by the influence of variation among years (Table 3) due to a small peak in prevalence in 2004 (Fig. 1). The best models of *Phobocampe* sp./*S. crassifemur* in both hosts and *A. flaveolatum* in



**Fig. 1.** Estimates of altitude and year-specific host densities (log-scale, number of larvae per 10 branches) and rates of parasitism (prevalence rates) for the five parasitoid species (or species groups) that were analysed. Error bars represent 95% confidence intervals.

*O. brumata* included the interaction between year and altitude (Table 3). *Phobocampe* sp./*S. crassifemur* showed similar temporal dynamics and prevalence ranges in the two host species (Fig. 1) with a distinct peak in 2002. The prevalence rates diverged most between the altitudes when the prevalences had their temporal peaks (Fig. 1). A similar altitudinal divergence at peak prevalence rates was evident for the generalist *A. flaveolatum* and the specialist *C. titubator* in *O. brumata* (Fig. 1). The latter parasitoid displayed increasing prevalence with altitude and a small peak in 2004 (Fig. 1).

#### Co-variation in generalist parasitoids among host species

Consistent with the tendency for similar temporal dynamics of *Phobocampe* sp./*S. crassifemur* in both hosts evident from Fig. 1, the spatio-temporal co-variation in the prevalence of this parasitoid was significantly positive [logistic regression on year and altitude-specific logit estimates; intercept = 1.69 ( $\pm 3.5$ ), slope = 0.76 ( $\pm 0.62$ ),  $P = 0.03$ ]. Moreover, the concurrent *Phobocampe* sp./*S. crassifemur* prevalence estimates were in most cases higher for *O. brumata* than for *E. autumnata* (i.e. the estimates tended to be below the diagonal in Fig. 2a). For the other generalist parasitoid, *A. flaveolatum*, there was an even clearer pattern for higher rates of parasitism in *O. brumata* than in *E. autumnata*.

However, in this case, no clear co-variation occurred among the hosts [logistic regression; intercept = 2.17 ( $\pm 8.16$ ), slope = 0.82 ( $\pm 1.21$ ),  $P = 0.2$ ] (Fig. 2b). Finally, there was a significant positive co-variation between the two hosts in total parasitoid prevalence (i.e. the summed mortality rates caused by all parasitoids) [logistic regression; intercept = 4.24 ( $\pm 4.68$ ), slope = 1.07 ( $\pm 0.89$ ),  $P = 0.04$ ], indicating relatively balanced parasitism rates in the two geometrid hosts across years and altitudes (Fig. 2c).

#### Parasitoid dependence on host density

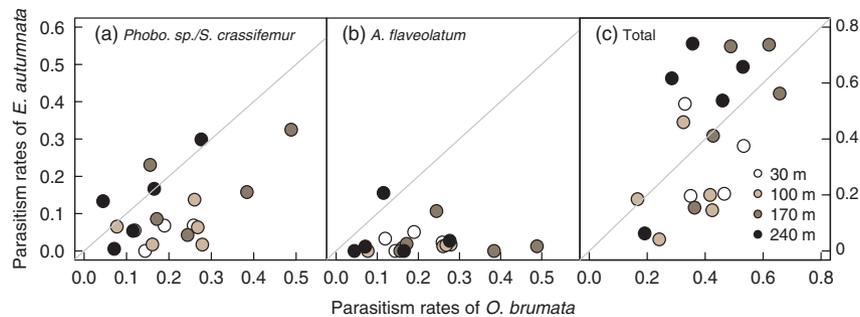
In general, there was only weak evidence for the strong spatio-temporal patterns in parasitoid prevalence rates (Fig. 1, Table 3) to be related to host densities (Fig. 3a,b). In *O. brumata*, all three parasitoid species/groups showed tendencies for a direct (i.e. spatial) response to host density. The same was the case for *Z. deceptor* in *E. autumnata* that also had a significant direct temporal ( $t - 1$ ) response. Only one parasitoid (*Phobocampe* sp./*S. crassifemur* in *O. brumata*) showed a tendency for positive delayed density-dependent relation to host density with a 2-year time lag, but the statistical significance of this relationship was mainly due to one low (i.e. outlying) estimate of parasitism (Fig. 3b). In all cases the scatter in the relations between parasitism and host density was large with a small amount of variation that could be attributed to density dependence (Fig. 3).

## Discussion

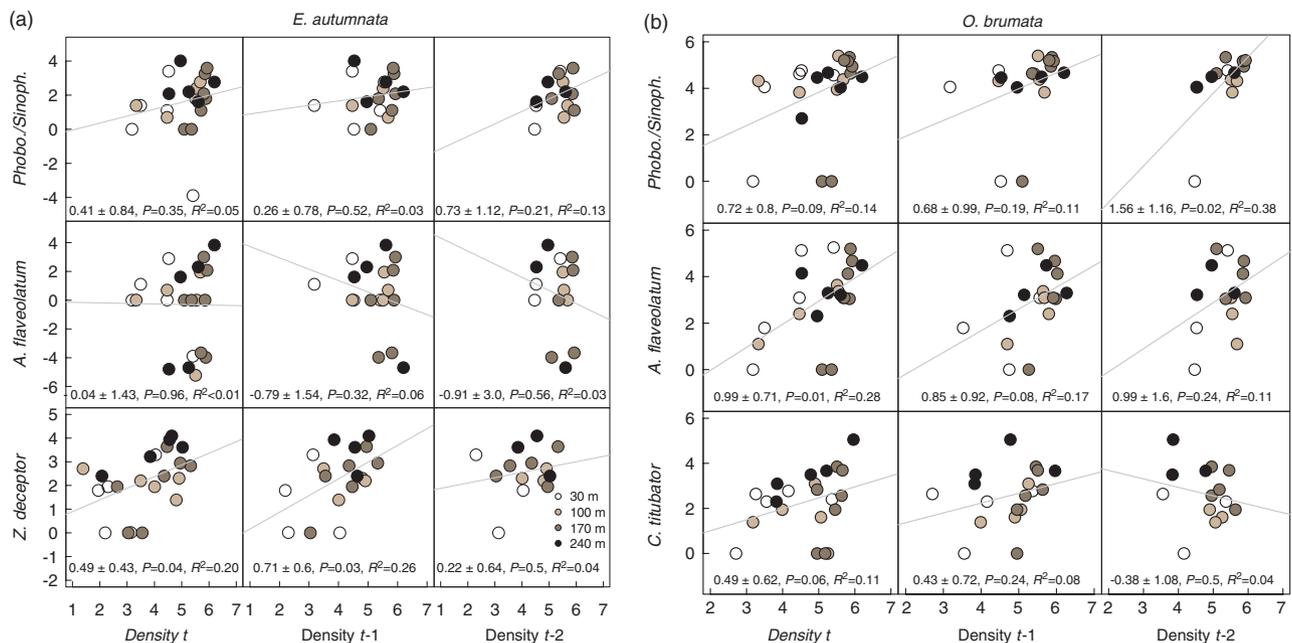
Population crashes of *E. autumnata* and *O. brumata* in the coastal birch forest of northern Norway have recently been found not to be caused by the action of larval parasitoids (Hagen *et al.*, 2010; Schott *et al.*, 2010). These studies concluded that parasitoid-induced larval mortality, which may reach high rates (cf. Fig. 2c), does not impact geometrid population growth rates. In the present study, we tried to uncover why larval parasitoids are incapable of regulating their hosts. We did so by investigating the specific nature of the spatial and temporal dynamics of each of the most abundant larval parasitoids in the two geometrid hosts. Our study design encompassed substantial variation in the density of the two host species (including the late increase, peak, and crash of their density cycles) as well as a spatial environmental gradient (i.e. altitude) decisive for outbreak amplitude. This allowed us to assess to what extent the parasitoids responded numerically or functionally to the two host species (i.e. in terms of density dependence) and whether there were patterns in prevalence rates that could indicate strong influences of other factors in their environment.

#### Spatio-temporal variation in parasitism independent of host density

We found that parasitism rates of all larval parasitoid species were distinctly patterned according to year and altitude. The



**Fig. 2.** Scatter plots depicting the degree of spatial-temporal correspondence between host species-specific parasitism rates. Panels (a) and (b): the two generalist parasitoid species/species groups. Panel (c): total parasitism. Data points above the grey line indicate higher rates of parasitism for *E. autumnata* and vice versa for *O. brumata*.

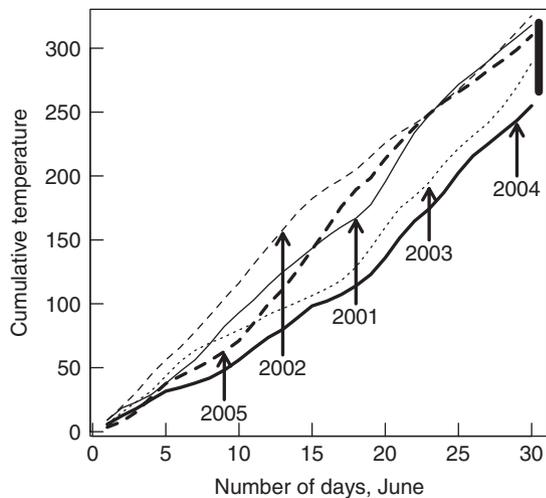


**Fig. 3.** Regression plots of logit parasitism of different parasitoid species and species groups in *E. autumnata* (a) and *O. brumata* (b) for logarithms of current ( $t$ ) and previous year host densities ( $t - 1$  and  $t - 2$ ). Dots are year-specific estimates for the four altitudes sampled. Lines, slope estimates,  $R^2$  and  $P$ -values are from linear regression models.

fit of the statistical models (as evaluated by Nagelkerke's  $R^2$ ) showed that there was hardly any extra-binomial variation left to be explained by other factors (i.e. 1–18%, Table 3), such as sampling station-specific spatial or temporal variation in host density. However, variables such as year and altitude cannot be attributed unambiguously to ecological mechanisms because there may be many ecological covariates. Host density also varied distinctly between altitudes and years (Fig. 1) but the density-dependent relationships between parasitoids and hosts were generally vague (*sensu* Strong, 1986) and mostly limited to some instances of non-delayed density dependence. Thus, it can be concluded that these parasitoids were not responding consistently to temporal density fluctuations in their hosts. Moreover, nothing in the present results (see Fig. 3a,b) suggests that parasitoids were more or less detached from host dynamics close to the alpine tree line so as to cause larger

outbreaks at high altitudes (Hagen *et al.*, 2007). Finally, this study rejects the possibility that host preferences for *E. autumnata* in generalist parasitoids (cf. Klemola *et al.*, 2009) could be involved in the temporal lag between *O. brumata* and *E. autumnata* population cycles. Both generalist parasitoids in the present study were found to be most prevalent in *O. brumata*, whereas total parasitism was fairly similar in the two species.

Altogether, the strong spatio-temporal patterns in the parasitoids and their hosts demonstrated here appeared to be largely independent of each other. Consequently, it can be suggested that the prevalence of larval parasitoids in birch forest geometrids is mainly ruled by other factors than the density of their hosts. This explains why larval parasitoids are not capable of regulating their hosts (Schott *et al.*, 2010). Such putative factors are discussed in turn below.



**Fig. 4.** Annual variation in cumulative June temperature throughout the study period. Data were taken from a weather station located in Tromsø, approximately 60 km south of the sample site. The respective dates of larval sampling are marked by arrows. The bar in the upper right corner indicates the expected difference in temperature sums between the lowest and highest altitude based on an orographic effect of  $0.6^{\circ}$  per 100 m.

#### Stochastic climatic variation

A wide range of stochastic abiotic variables has been shown to negatively impact parasitoid host search efficiency and general performance. Examples include temperature (Taylor, 1981; Bale, 1993; van Roermund & van Lenteren, 1995; Bouchier & Smith, 1996; Fournier & Boivin, 2000), barometric pressure (Steinberg *et al.*, 1992; Fournier & Boivin, 2000), wind velocity (Weisser *et al.*, 1997; Fournier & Boivin, 2000; Gu & Dorn, 2001) and precipitation or humidity (Bouchier & Smith, 1996; Weisser *et al.*, 1997). All these factors certainly vary across years and altitudes (Körner, 2007). Among climate variables only daily temperatures from a meteorological station 60 km away from the sites were available for direct evaluation of climatic variation in the temporal domain of this study. However, temperatures are strongly correlated well beyond such a distance in this region (Tveito *et al.*, 2000) so the measurement from this station should be representative. Cumulative temperatures covering activity (i.e. flight) periods of potentially egg laying parasitoids show that 2003 and 2004 were relatively cold compared to the three other years (Fig. 4). While some parasitoids had overall low prevalence rate in the two coldest years (e.g. *Z. deceptor* and *Phobocampe* sp.*S. crassifemur*), the temporal patterns related to simple temperature sums cannot readily be reconciled with altitudinal prevalence patterns. For instance, *Phobocampe* sp.*S. crassifemur* was found to be most prevalent at the highest and coldest positions in the altitudinal gradient. With respect to the likelihood of spatio-temporally variable phenological matching between parasitoids and susceptible larval stages, it is important to note that *E. autumnata* is expected to hatch up to 10 days before *O. brumata* in the range of temperatures experienced during the present study (Jepsen *et al.*, 2011). Despite this

phenological asynchrony between the host species, there was a consistent correlation in host-specific prevalence rates across years and altitudes in the most numerous generalist parasitoid group (*Phobocampe* sp.*S. crassifemur*). This suggests that the degree of matching between larvae and parasitoids is not very sensitive to climatic variation. Temperature-induced phenological mismatch was also deemed to be quite unlikely in a more detailed study of parasitoid and host phenology in population outbreaks of *O. brumata* (Vindstad *et al.*, 2011).

However, while some putative disrupting climatic mechanisms, such as phenological matching between hosts and larval parasitoids, appear unlikely in the present case, other unknown climatic mechanisms may be important. In particular, nothing is known about the climate sensitivity of these parasitoids during life stages not encompassing the larval stage of their hosts. Hence, it is possible that climatic variation during other seasons and life stages shapes parasitoid population dynamics so as to uncouple them from the dynamics of their geometrid hosts. Moreover, we have no data on local episodes of weather phenomena such as strong winds, which could cause differences among altitudes.

#### Biotic interactions

There may be a host of interactions in the food web beyond those between herbivores and their parasitoids (Eveleigh *et al.*, 2007). Some of them, such as the action of hyper-parasitoids, predators, and parasites/diseases on other host life stages, may potentially disrupt the link between geometrids and their larval parasitoids. Complex (non-linear) trophic interactions can easily bring about rapid temporal transitions in population dynamics and food web structure (Abrams *et al.*, 1998; Hastings, 2004). We have very limited knowledge of the extent of such interactions. What is required first of all is a much more complete map of the food web (cf. Eveleigh *et al.*, 2007; Ings *et al.*, 2009). Using such a map, it would be interesting to compare whether complexity differs between coastal and continental forests, for which the role of larval parasitoids in geometrid population dynamics appears to differ.

#### Lottery processes

As can be seen from the prevalence dynamics of the individual parasitoid species or species groups, substantial temporal turnover in the structure of the parasitoid guild (dominance relations between species) could take place from one year to the next. Similarly, Vindstad and colleagues (2010) found the structure of the same parasitoid guild in *O. brumata* to show substantial spatial turnover along a 70 km transect running through the fjord district at relatively low altitudes about 40 km south-east of our study site. Vindstad and colleagues proposed that the parasitoid guild could be structured according to a lottery model (Tokeshi, 1999), by which the guild is stochastically restructured by (near) extinctions and recovery of parasitoids after cyclic crashes of their host populations. Correspondingly, one would not expect large temporal changes in parasitoid guild structure in the late

increase phase and peak phase of the host population. As the study of Vindstad and colleagues was based on a snapshot of large-scale spatial patterns in one outbreak year they could not further evaluate this hypothesis. However, the present study demonstrating major temporal changes in the structure of the parasitoid guild towards the peak of the host cycle, calls for other explanations than a stochastic lottery process.

## Conclusion

The guild of larval parasitoids in the two sympatric cyclically outbreaking geometrids in coastal birch forest in northern Fennoscandia exhibits strong multi-annual prevalence dynamics, which are spatially structured along altitudinal gradients. However, these spatio-temporal dynamics appear to be little shaped by parasitoid–host interactions. Factors responsible for such a large degree of disentangled parasitoid–host dynamics should be sought in unknown climate sensitivity in the parasitoids or biotic mechanisms not involving host populations.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

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**Table S1.** Parameter estimates for the selected models for the prevalence of larval parasitoid species in *E. autumnata*.

**Table S2.** Parameter estimates for the selected models for the prevalence of larval parasitoid species in *O. brumata*.

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