

# Spatially patterned guild structure in larval parasitoids of cyclically outbreaking winter moth populations

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**Abstract.** 1. Wide temporal fluctuations in host abundance are a potential source of instability and stochasticity in the spatiotemporal population dynamics of associated parasitoid species. Within parasitoid guilds (i.e. parasitoids with similar modes of host utilisation), a conceivable outcome is guild organisation according to a lottery model, in which guild members attain local dominance by colonising previously emptied habitats during increasing host density, before other guild members. In the spatial dimension, an expected manifestation of such dynamics is variable guild structure even across homogeneous habitats.

2. We examined the extent of large-scale spatial patterning of guild characteristics in larval parasitoid wasps associated with cyclically outbreaking populations of the geometrid moth *Operophtera brumata* in northern Fennoscandia. The study was performed at the onset of the crash-phase of the geometrid's outbreak cycle, along a 70-km transect in coastal northern Norway, characterised by largely homogeneous environmental conditions, except for a small climatic gradient.

3. There was a distinct large-scale spatial turnover in dominance among the major parasitoid groups (i.e. guild structure) in *O. brumata* along the transect, whereas the total prevalence rate of the guild and its diversity showed no consistent variation. Guild structure was unrelated to host density.

4. Although group-specific responses to a slight spatial climatic gradient cannot be rejected as a causal mechanism, we conclude that our results are consistent with the expectation from large-scale stochastic extinction-recolonisation dynamics among functionally equivalent parasitoids relying on a host with strongly cyclic population fluctuations.

**Key words.** Competitive lottery, founder-control, host population cycles, spatial community structure, stochasticity.

## Introduction

The prevalence of individual parasitoid species within a given species of host can sometimes exhibit pronounced large-scale spatial variation. Typically, such spatially structured prevalence patterns are interpreted in terms of deterministic processes, including species-specific responses to spatial variation in climate (Kato, 1996; Virtanen & Neuvonen, 1999), landscape structure (Roland & Taylor, 1997), host food plants (Craig, 1994) or the abundance of host species (Mills, 1994; Stireman

& Singer, 2002). However, in systems where local parasitoid populations are destabilised by strong temporal fluctuations in host abundance, stochasticity in processes of parasitoid extinction, dispersal, and recolonisation might also give rise to spatially structured prevalence patterns. Particularly among parasitoids forming guilds with similar modes of host utilisation and potentially strong competitive interactions, it is conceivable that local dominance under such unstable conditions is decided by a 'competitive lottery' (Tokeshi, 1999 and references therein) which leads to 'founder-controlled' guilds (Begon *et al.*, 2006). In the lottery model, guild members are functionally and competitively equivalent and any of them can attain dominance locally by establishing before intra-guild competitors in unexploited habitats. Habitats

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are opened by stochastic extinction of former dominants, for instance caused by population crashes in the host population. Establishment and extinction is assumed to be equally probable among guild members, thus making stochasticity in demographic processes the main factor in deciding which species attain local dominance. Hence, an expectation from the lottery model is that the prevalence of individual guild members and structure (composition) of the guild at any given time is likely to become variable even across a homogeneous habitat.

As outlined above, parasitoids forming guilds in host species with strongly fluctuating populations in large tracks of homogeneous habitats would be suitable cases for expecting and detecting spatial prevalence patterns resulting from stochastic lottery processes. In the North-Fennoscandian mountain birch (*Betula pubescens czerepanovii*) forest, the larval parasitoid wasps of the defoliating geometrid moths (Lepidoptera: Geometridae) *Epirrita autumnata* (Bkh.) (Autumnal moth) and *Operophtera brumata* (L.) (Winter moth) are prime examples of parasitoid guilds associated with temporally fluctuating hosts. In this system, both geometrids exhibit regionally synchronised, high amplitude 9–10 year population cycles with extremely low densities in the low phases of the cycle (Tenow, 1972; Ruohomäki *et al.*, 2000). Larval parasitoids show strong numerical responses to these fluctuations (Tanhuanpää *et al.*, 2002; Klemola *et al.*, 2008 and references therein), thus making local extinctions likely. Studies of larval parasitism in *E. autumnata* have suggested the prevalence of different larval parasitoid species to differ substantially between locations (Ruohomäki, 1994; Kaitaniemi & Ruohomäki, 1999; Virtanen & Neuvonen, 1999). However, none of these previous studies were designed so that it could be assessed whether deterministic or stochastic processes were likely to underlie the spatial variability.

In the present study, we attempted to fulfil the conditions for assessing whether spatial patterning in larval parasitoid guild structure is consistent with a stochastic lottery model. We estimated parasitoid prevalence rates and abundances of hosts (i.e. geometrid larvae) according to a systematic, large-scale transect design (70 km). The sampling transect ran through a homogeneous belt of coastal birch forest at fixed altitudes, so that the variation in environmental conditions was expected to be minimal. Moreover, the sampling was conducted during

the onset and early stages of the crash-phase of the regional geometrid outbreak cycle. Thus, the parasitoid guild was expected to be in the same stage of succession series.

## Materials and methods

### Study species

*E.* and *O. brumata* are polyphagous univoltine geometrid moths with Holarctic distributions and a largely similar biology. In our study area in northern Norway, adults of *E. autumnata* emerge from buried pupae in mid August to September, whereas emergence of *O. brumata* occurs about a month later (Peterson & Nilssen, 1998). Females oviposit in trees and eggs overwinter to hatch in synchrony with budburst the subsequent spring. The larval stage spans five instars and typically has a duration of about 1 month in our study area. After larvae have completed their development, pupation occurs in the soil. The main host plant for larvae of the two geometrid species in northern Fennoscandia is the mountain birch (Tenow, 1972).

In our study area, all known larval parasitoids of *E. autumnata* and *O. brumata* are Hymenopteran univoltine koinobionts [with the possible exception of *Protapanteles* species, which show bivoltinism in other locations (Teder *et al.*, 2000)]. Eclosion from hosts happens either during the late larval stage (early-eclosing species) or after host pupation (late-eclosing species). The biology of most parasitoid species is poorly known, but a summary of major characteristics is given in Table 1. The parasitoids associated with *E. autumnata* and *O. brumata* have been suggested to exhibit functional specialism on one or both of these geometrids in northern Fennoscandia, as a result of paucity of alternative host species in this region (Klemola *et al.*, 2002, 2007, 2009 and references therein).

### Study area and sampling design

The study was conducted in 2005 within a continuous belt of homogeneous mountain birch forest around the fjord

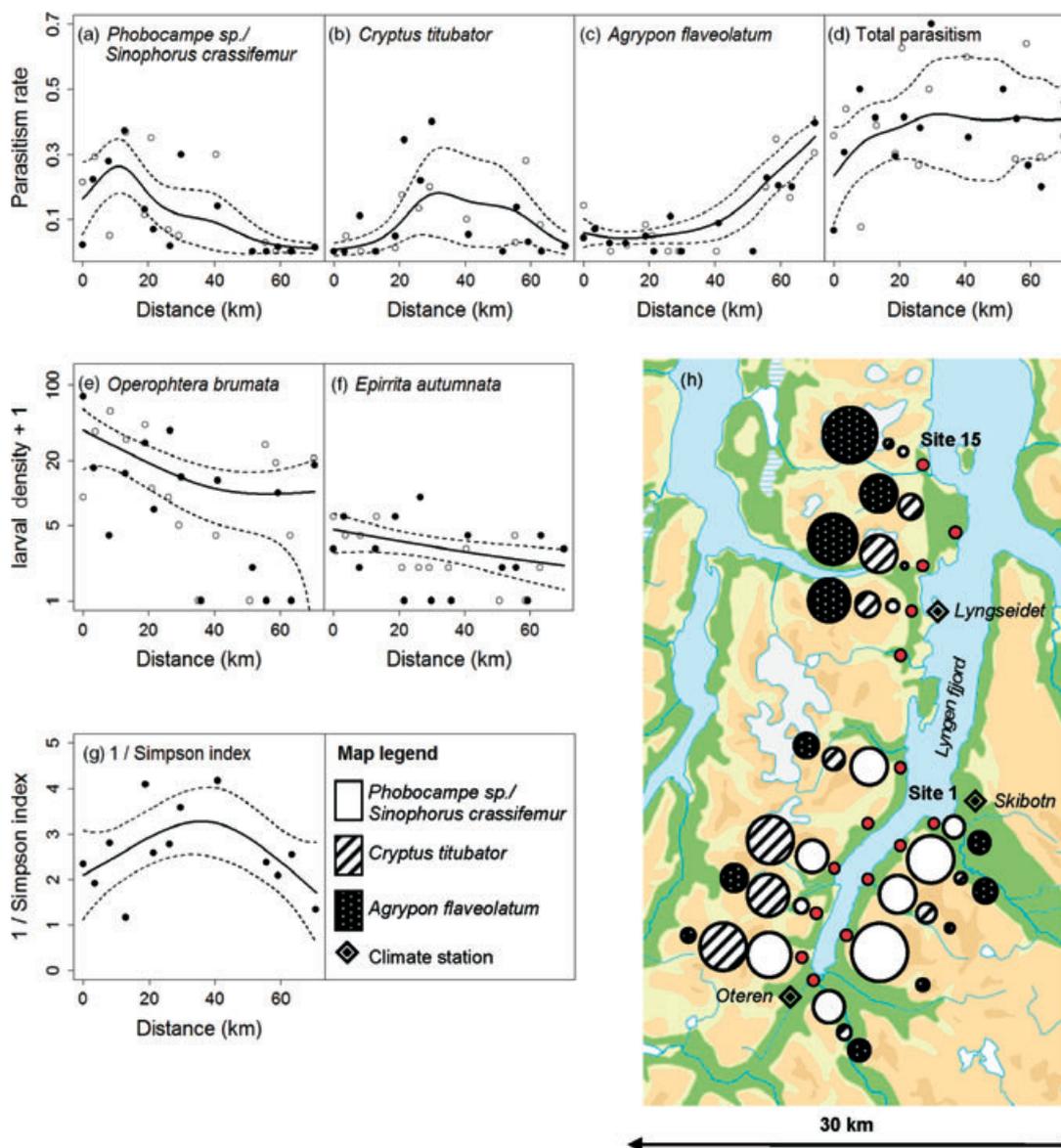
**Table 1.** Characteristics of the individual parasitoid species/groups encountered in the study.

Parasitoid species/group	Family	Eclosion	Development in/on host	Host species
<i>Agrypon flaveolatum</i>	Ichneumonidae	Late	Solitary endoparasitoid	OB + EA
<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i>	Ichneumonidae	Early	Solitary endoparasitoid	OB + EA
<i>Cryptus titubator</i>	Ichneumonidae	Late	Solitary endoparasitoid	OB + EA
<i>Protapanteles anchisiades</i> / <i>P. immunis</i> / <i>Cotesia salebrosa</i>	Braconidae	Early	Solitary endoparasitoid	OB + EA
<i>Aleiodes gastritor</i>	Braconidae	Early	Solitary endoparasitoid	EA
<i>Zelex deceptor</i>	Braconidae	Early*	Solitary endoparasitoid	EA
'Yellow cluster'	Braconidae	Early	Gregarious endoparasitoid	OB
<i>Eulophus larvarum</i>	Eulophida	Early	Gregarious ectoparasitoid	OB + EA

\*Ecloses from host larvae that have ceased feeding and are preparing for pupation.

Early-eclosing groups emerge from host larvae, whereas late-eclosing groups emerge from host pupae.

OB, *O. brumata*; EA, *E. autumnata*.



**Fig. 1.** (a–g) Predicted values (solid lines)  $\pm$  2 SE (dashed lines) from generalised additive models (GAMs) relating group-specific (a–c) and total (d) parasitism rates, larval densities (e–f) and Simpson index values (g) to over-land distances from sampling-site one. Original data values are shown as hollow and solid circles for 30 and 100 m.a.s.l. sites, respectively, in the case of parasitism rates and larval densities, and as solid circles for the Simpson index, where data were pooled over the two altitudes. (h) Map of the study area, showing the location of climate stations and the 15 sampling-sites (red dots). The size of the circles are proportional to the site-specific parasitism rates (pooled over 30 and 100 m.a.s.l.) of the three major parasitoid groups of *Operophtera brumata*.

Lyngenfjorden, located in Troms County in northern Norway. The region is characterised by oceanic climate, with mild winters (mean January temperature  $-2$  to  $-5$  °C) and moist, cool summers (mean July temperature  $10$ – $12$  °C) (Tveito *et al.*, 2000). We used a 70-km-long transect consisting of 15 more or less evenly spaced sampling-sites (Fig. 1h), each with a sampling station at 30 and 100 m.a.s.l. To assess the extent of climatic variation along the transect, we obtained data on annual and monthly averages of temperature and precipitation from climate stations close to site 1 (Skibotn), 5 (Oteren), and

12 (Lyngseidet) from the Norwegian Meteorological Institute (<http://www.met.no>) (Fig. 1h, Appendix S1).

Larvae for parasitoid rearing were sampled on 6 July at all sites. At this time, larvae were in the fourth to fifth instar with a high degree of uniformity along the transect and between altitudes. Phenological biases in the spatial patterning of parasitism rates were thus expected to be minimal. We sampled late instars, although well ahead of pupation, to allow a majority of parasitoid attacks to occur before sampling and simultaneously minimise the loss of parasitoid species that

eclose late in the larval stage (Teder *et al.*, 2000). Larvae were collected by shaking branches of haphazardly chosen birch trees in a large plastic box. Larval densities were estimated in a similar manner 1 week in advance of larvae collection, by counting the number of dislodged larvae after shaking ten 80-cm birch branches, collected haphazardly within a radius of 20 m around the sampling stations (Hagen *et al.*, 2010).

In 2005, most *O. brumata* populations along the transect had entered the onset of the population cycle's crash phase, whereas the *E. autumnata* populations had proceeded to a somewhat more advanced stage of the crash (see Hagen *et al.*, 2010, fig. 2). Although being in approximately the same phase of the cycle within species, the abundance of geometrid larvae varied substantially along the transect (Fig. 1e,f) resulting in sample sizes ranging from 3 to 166 larvae per site for *O. brumata* (Appendix S2) and 2–20 larvae per site for *E. autumnata*. No larvae were obtained for parasitoid rearing from site 11 at 30 m and site 9 at both altitudes. Sampled larvae with unknown fate or unidentified mortality were omitted from the sample and a total of  $n = 1368$  *O. brumata* larvae and  $n = 242$  *E. autumnata* larvae entered the analyses.

#### Rearing of larvae

Sampled larvae were reared at  $\approx 20^\circ\text{C}$  in groups of maximally 20 individuals in 1-l ( $8 \times 15 \times 8$  cm) plastic boxes, containing a layer of silted soil for pupation and some peat moss (*Sphagnum spp.*) to retain moisture. Feeding with freshly clipped birch leaves and recording of early-eclosing parasitoids was done every third day. After pupation, the boxes were stored outdoors under ambient temperature conditions, sheltered from direct sunlight and precipitation. Pupae that failed to hatch were dissected for late-eclosing parasitoid species.

#### Identification of parasitoids

Emerged parasitoids were classified based on cocoon morphology. Identification of adult specimens by Finnish taxonomists was arranged by Kai Ruohomäki at the University of Turku in Finland. The identity of some specimens could not be established with certainty. It is, therefore, possible that some of the parasitoids classified into one single taxonomic unit in reality represent an assemblage of different species with similar morphology. The term parasitoid 'group' (Schott, 2007) will, therefore, be used in this paper as a substitute for parasitoid 'species'. A very uncommon small gregarious Braconid parasitoid could not be identified and will be referred to as 'Yellow cluster'.

#### Data analysis

Parasitism (i.e. prevalence) rates were taken as  $p = np/n$ , where  $n$  is the number of cultured larvae and  $np$  is the number of larvae parasitised. These rates were considered for all parasitoid groups individually and collectively, for each individual sampling-site and for the transect as a whole. As a result

of very low population densities, the site-specific samples of *E. autumnata* were too small to allow for analyses of spatial patterns. Hence, for this host species, only overall parasitism rates (and parasitoid guild structure) for the whole transect will be presented to allow a broad comparison between the two geometrids.

The reciprocal of the Simpson index ( $D$ ) was used as a measure of diversity within the larval parasitoid guild of *O. brumata*. This measure takes higher values with increasing evenness in the abundances of the species in a sample (i.e. the dominance relations) (Magurran, 2004). Site-specific values were taken as  $1/D_j = 1/\sum(np_{ij}[np_{ij} - 1]/np_j[ np_j - 1])$ , where  $np_j$  is the total number of parasitised larvae from site  $j$  and  $np_{ij}$  is the number of larvae from site  $j$  parasitised by parasitoid group  $i$ . Data from the 30-m and 100-m sampling stations were pooled for these calculations, to ensure adequate sample sizes for estimation of the index. One site (11) where only a single larva was found to be parasitised was omitted.

We employed generalised additive models (GAMs) (Wood, 2006) to characterise the spatial patterning of three groups of response variables along the transect: (i) total and group-specific parasitism rates of *O. brumata*, modelled with logit link-function and binomial error distribution, (ii) Simpson index for the larval parasitoid guild of *O. brumata*, modelled with identity link-function and normal error distribution, and (iii) larval densities of both host species, modelled with log link-function and Poisson error distribution. In all GAMs, over-land distances from the first sampling-site (hereafter 'distance') were specified as a smoothed non-parametric predictor variable. Thus, it was assumed that the fjord acted as a dispersal barrier for both parasitoids and larvae. Fitting separate GAMs for 30- and 100-m sites showed that the spatial patterning of all parasitism rates and larval densities was very similar between the altitudes. A single GAM fit for both altitudes was, therefore, considered adequate for characterisation of spatial patterns in all groups of response variables. Altitude was still added as a parametric covariate to the models of parasitism rates and larval densities, to explore the possibility of consistent altitudinal variation in these variables for the transect as a whole. Penalised thin-plate regression splines were used as a basis for the smooths in all cases. We derived approximate significance levels for the smooth terms according to the methodology described in Wood (2006), using the quasi-likelihood approach recommended in the case of unknown scale parameters for the models assuming binomial and Poisson error structures. The automatic selection of the smoothing parameter ( $\lambda$ ) based on generalised cross validation (GCV) provided by mgcv package in R (Wood, 2006) appeared to provide appropriate results for the modelling of larval density and Simpson index. However, it produced an excessively complex fit for one of the major parasitoid groups (*Cryptus titubator*). We, therefore, chose to override this selection procedure and manually set  $\lambda = 0.1$ , as this provided a moderate degree of smoothing and thereby emphasised dominant patterns in the data without obscuring significant small-scale variation. We used the same  $\lambda$  value for modelling all parasitism rates, in order to ensure comparability of the individual models.

To investigate whether local host density affected the prevalence of individual parasitoid groups of *O. brumata*, we conducted logistic regressions using site-specific *O. brumata* densities as the predictor variable, and site-specific parasitism rates for each group as the response variables. Although *E. autumnata* is a potential host for most of the parasitoid groups encountered in the study, densities of this geometrid along the transect were too low and uniform to make them meaningful as an additional predictor in the models. To investigate the relationship between overall larval parasitism rates of *O. brumata* and the diversity of the larval parasitoid guild, we also performed a logistic regression using the Simpson index as a predictor variable and site-specific total parasitism rates (pooled across both altitudes) as the response variable. Goodness-of-fit tests based on sums of squared Pearson residuals showed evidence of overdispersion for all logistic models ( $\chi^2 > 40.835$  and  $P < 0.001$  in all cases). This was corrected for by implementing quasi-binomial errors.

All statistical modelling was carried out with the statistical package R (R Development Core Team, 2006).

## Results

### Parasitoid guild structure according to host species

In total, eight groups of Hymenopteran larval parasitoids were recorded (Table 1). Two of these were specific to *E. autumnata*, one was specific to *O. brumata*, while five groups were recovered from both geometrid species. Despite the fact that *E. autumnata* and *O. brumata* shared a majority of the parasitoid groups, there were major deviations in the quantitative compositions of their larval parasitoid guilds (Table 2): *E. autumnata* was mainly parasitised by the two Braconids *Aleiodes gastritor* and *Zelex deceptor*, while the three Ichneumonids *Phobocampe* sp./*Sinophorus crassifemur*, *Cryptus titubator*, and *Agrypon flaveolatum* (hereafter the 'major parasitoid groups') collectively accounted for most

**Table 2.** Overall parasitism rates  $\pm 1$  SE of *Epirrita autumnata* and *Operophtera brumata* for the individual parasitoid species/groups encountered in the study.

Parasitoid species/group	Parasitism rate <i>O. brumata</i>	Parasitism rate <i>E. autumnata</i>
<i>Agrypon flaveolatum</i>	0.150 ( $\pm 0.022$ )	0.004 ( $\pm 0.004$ )
<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i>	0.124 ( $\pm 0.026$ )	0.062 ( $\pm 0.027$ )
<i>Cryptus titubator</i>	0.064 ( $\pm 0.022$ )	0.012 ( $\pm 0.011$ )
<i>Protapanteles anchisiades</i> / <i>P. immunis</i> / <i>Cotesia salebrosa</i>	0.018 ( $\pm 0.020$ )	0.004 ( $\pm 0.004$ )
<i>Aleiodes gastritor</i>	–	0.116 ( $\pm 0.027$ )
<i>Zelex deceptor</i>	–	0.157 ( $\pm 0.027$ )
'Yellow cluster'	0.001 ( $\pm 0.002$ )	–
<i>Eulophus larvarum</i>	0.018 ( $\pm 0.005$ )	0.058 ( $\pm 0.015$ )
<b>Total parasitism</b>	<b>0.376 (<math>\pm 0.030</math>)</b>	<b>0.413 (<math>\pm 0.050</math>)</b>

of the parasitism of *O. brumata*. Only the *Phobocampe* sp./*Sinophorus crassifemur* group showed relatively high prevalence in both geometrids.

### Spatial patterns and determinants of guild structure

The altitude term was non-significant in all GAMs of parasitism rates of *O. brumata* ( $P > 0.6$  in all cases) and could be excluded from the models without influencing the conclusions of the analysis. This showed that there was no consistent altitudinal variation in the prevalence of any major parasitoid group or of the larval parasitoid guild as a whole, despite considerable differences in both group-specific and overall prevalences between altitudes at some sites (Fig. 1a–d). The smooth term for distance was significant on approximately 3.5 estimated degrees freedom (e.d.f.) in the GAMs of all three major parasitoid groups (Table 3), demonstrating consistent and non-linear variation in the prevalence of each group

**Table 3.** Summary of statistics for the smooth term for over-land distance from sampling-site one in all generalised additive models (GAMs) fitted in this study, organised according to response variable.

Response variable group	Species/group	<i>n</i>	e.d.f.	Est. rank	F-value	Appr. P	Fig
Parasitism rate of <i>Operophtera brumata</i> *	<i>Agrypon flaveolatum</i>	27	3.568	8	15.020	<0.001	1a
	<i>Phobocampe</i> sp./ <i>Sinophorus crassifemur</i>	27	3.526	8	4.256	0.003	1b
	<i>Cryptus titubator</i>	27	3.321	7	2.643	0.037	1c
	Total parasitism	27	4.475	9	0.758	0.654	1d
Larval density†	<i>Operophtera brumata</i>	30	1.810	4	3.332	0.024	1e
	<i>Epirrita autumnata</i>	30	1.000	1	4.536	0.042	1f
Simpson index‡,§	<i>Operophtera brumata</i>	13	2.206	5	1.909	0.181	1g
	Parasitoid guild						

\* $\lambda$  Manually set to 0.1.

† $\lambda$  Selected automatically based on GCV.

‡Data from 30 and 100 m sampling-sites pooled.

E.d.f., estimated degrees of freedom; Est. rank, estimated rank of covariance matrix;

Appr. P, approximate significance level.

*n* refers to the number of data points on which the models are based.

Predicted values from each model are plotted together with original data values in the specified figures.

along the transect, with a clear tendency of large-scale spatial segregation between groups (Fig. 1a,b,c and h). *Phobocampe* sp./*S. crassifemur* was the most common group at the lower numbered sites, but became progressively rarer towards the middle of the transect and was virtually absent at sites 12–15 (Fig. 1a,h). These sites were mostly dominated by *A. flavolatum*, which in contrast was relatively rare at sites 1–10 (Fig. 1c,h). *Cryptus titubator* occurred mainly around the middle of the transect, in a zone somewhat intermediate between the main reaches of the two other major groups (Fig. 1b,h). The remaining three parasitoid groups of *O. brumata* were rare (generally <5% prevalence at all sites) and were, therefore, not subjected to individual analysis.

Distance was non-significant in the GAM of total parasitism rates (Table 3), indicating that there was no consistent large-scale variation in prevalence of the larval parasitoid guild as a whole along the transect (Fig. 1d). The same was true for the GAM of the Simpson index (Table 3), indicating that there were no consistent changes in the diversity of the guild along the transect [although there was seemingly a tendency for the diversity index to take somewhat higher values around the central sites, in the zone of transition between the three major parasitoid groups (Fig. 1g)]. Logistic modelling of total parasitism rate showed that this response variable was not related to larval parasitoid diversity ( $F_{1,11} = 1.000$ ;  $P = 0.339$ ).

Altitude was non-significant ( $P > 0.7$  in both cases) and was excluded from the GAMs of larval density of both geometrids. The smooth terms for distance were significant on 1.00 and 1.81 e.d.f. for *E. autumnata* and *O. brumata* respectively (Table 3), and described monotonous declines in larval density with increasing distance from site one in both geometrids (Fig. 1e and f). Logistic modelling of group-specific parasitism rates showed that *O. brumata* density did not significantly explain the prevalence of any of the three major parasitoid groups ( $F_{1,25} < 1.944$ ;  $P > 0.176$  for all groups).

## Discussion

Previous studies of larval parasitism in *E. autumnata* have suggested that larval parasitoid guilds associated with North-Fennoscandian birch forest geometrids exhibit a spatially variable species composition (Ruohomäki, 1994; Kaitaniemi & Ruohomäki, 1999; Virtanen & Neuvonen, 1999). No other studies have, however, been able to quantify the spatial scale of such variation or attempted to infer causal mechanisms by relating it to internal guild characteristics, host density, or particular environmental factors except altitude in the study of Virtanen and Neuvonen (1999). By employing a specific transect design, we were able to document a large-scale, gradual spatial turnover in dominance among the major larval parasitoid species (or species groups) of *O. brumata* across a 70-km distance in costal northern Norway. Interestingly, this distinctly patterned guild structure appeared to be unrelated to other guild characteristics (diversity and overall prevalence of larval parasitoids) as well as host density and any environmental factors

that we were able to control for by the sampling design. Moreover, Hagen *et al.* (2010) showed that host population dynamics in this system were unrelated to the rate of larval parasitism.

Because we designed our study to minimise environmental variation, we can reject most of the deterministic explanations that typically are proposed to account for spatial variation in parasitoid species composition within a given species of host. First, effects related to the identity of host food plants (Craig, 1994) can be ruled out, as all larvae were sampled on mountain birch trees within a homogeneous belt of mountain birch forest. The high degree of homogeneity and continuity of the forest also argues against an important role of forest structure (Roland & Taylor, 1997) in organising the studied parasitoid guild. Current-year host density (Price, 1971; Mills, 1994) had no effect on the prevalence of any of the major parasitoid groups, and we are not aware of any alternative host species occurring in sufficient densities to influence parasitoid attack rates on *O. brumata* (Stireman & Singer, 2002). Altitudinal effects (Kato, 1996; Virtanen & Neuvonen, 1999) can be disregarded, as this was controlled for in our design. The overall (i.e. for the transect as a whole) independence between larval parasitoid guild structure and altitude in our study may, however, be due to the rather small range of altitudes, as Virtanen and Neuvonen (1999) found the species composition of larval parasitoids in *E. autumnata* to vary substantially along a more extensive altitudinal gradient. Note, however, that spatial patterns resulting from a stochastic lottery process could easily lead to spurious correlations with environmental gradients. Indeed, the parasitoid prevalences in our study exhibited considerable seemingly random within-site altitudinal variation that may well have resulted from local lottery processes, although much of this variation was probably also because of sampling error. Climate data at the level of our individual sampling sites is unavailable, but measurements from more widely spaced climate stations suggest the presence of slight gradients in temperature and precipitation along the transect (Fig. 1h. Appendix S1). This climatic variation appears rather modest compared with the pronounced spatial segregation of the three major parasitoid groups of *O. brumata* in this study, but nevertheless cannot be ruled out as a causal mechanism, as the climate sensitivities of the parasitoids are unknown.

Although a deterministic explanation based on spatial climatic variation cannot be rejected, the distinct large-scale spatial patterning of the focal guild of parasitoids across an otherwise homogenous habitat can also be interpreted as being consistent with the expected outcome of a stochastic lottery model. Perhaps somewhat surprising is the relatively large-scale nature of the spatial patterns found. However, large-scale prevalence patterns could develop if parasitoids of different species are extant only in widely dispersed locations after host population crashes and that such locations become epicentres for gradual expansion of parasitoids through the stages of increase and peak of the host population cycle. Such a scenario is based on a rather low and equal mobility of the parasitoids forming the guild. Indeed, the lottery model assumes a high degree of functional equivalence among the guild members. The major parasitoid groups in the study are all relatively large, solitary Ichneumonids, so the assumption

of functional equivalence (mobility and efficiency of host utilization) seems realistic. Moreover, functional equivalence among guild members is also compatible with the finding that the prevalence of the guild as a whole (i.e. total prevalence) was independent of its structure (i.e. which guild member was dominant) and the overall dominance relation within the guild (guild diversity). Note, however, that the scenario proposed above is not a competitive lottery in the strictest sense, i.e. that species compete for empty habitats and the first to establish retains local dominance in the face of later arriving competitor species. However, the model proposed in the present case is similar in concept by emphasising stochasticity in processes of extinction and dispersal as the key mechanism in deciding which species dominate locally. This model may also be more realistic than strict-sense lottery competition, in the sense that it could give rise to spatially structured prevalence patterns without single parasitoid species being able to monopolise local habitats and their hosts. Such a monopolisation of hosts appears to be unlikely at the peak of the geometrid population cycle, when parasitoids are likely to be swamped by a high host density (i.e. note that on average less than half of the host larvae were parasitised in the present study).

Altogether, our research at the present stage points towards the possibility that stochastic processes may be important determinants of large-scale prevalence patterns of larval parasitoids in these northern populations of birch forest geometrids, although we cannot dismiss the possibility that high sensitivity to climatic variation in the parasitoids could have played a role. If the former interpretation is true, it would also help explain why these natural enemies do not appear to regulate their host populations (Hagen *et al.*, 2010; Schott *et al.*, 2010). Clearly, however, the inferences that can be drawn from our pattern-oriented analysis are still limited by the fact that guild structure variation has as yet only been studied in the spatial domain. New studies incorporating temporal variation in parasitoid prevalence would shed further light into the relative importance of stochastic and deterministic processes in shaping the structure of these guilds.

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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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**Appendix S1.** Annual and monthly mean temperatures (°C) for the current climate normal period (1961–1990) for climate

stations at Lyngseidet, Skibotn, and Oteren (Fig. 1h). Annual and monthly mean precipitation (mm) for the current climate normal period (1961–1990) for climate stations at Lyngseidet, Skibotn, and Oteren (Fig. 1h).

**Appendix S2.** Altitude- and site-specific sample sizes (n) of *O. brumata* larvae. Note that the sample sizes refer only to larvae whose fate is known with certainty.

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