

Are population outbreaks in sub-arctic geometrids terminated by larval parasitoids?

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Summary

1. Larval parasitoids (i.e. parasitoids attacking host larvae) constitute a major source of mortality in many ecologically and economically important forest insects, but how this mortality affects spatio-temporal population dynamics is often not clear.
2. In sub-arctic Fennoscandian birch forest, the two geometrids *Epirrita autumnata* and *Operophtera brumata* exhibit pronounced outbreak cycles with significant ecosystem impacts. As mortality owing to larval parasitoids often is very high, the hypothesis that parasitism terminates outbreaks has been advocated, but without decisive empirical evidence.
3. We analysed the altitude- and species-specific timing of population outbreaks typically seen in the coastal section of the sub-arctic birch forest ecosystem to evaluate the critical premise that parasitoid-inflicted larval mortality ought to predict geometrid population growth.
4. However, despite temporally high rates of parasitism, this did not influence the strongly species- and altitude-patterned geometrid outbreaks. We therefore conclude that termination of cyclic outbreaks in these geometrids is caused by other regulatory mechanisms than larval parasitoids.
5. Regardless of their lack of effect on the altitude-specific outbreak dynamics, larval parasitoids accounted for some of the local spatial variance in the temporal dynamics. This implies that results from spatially localized observations and experiments, which dominate research on parasitoid–host interaction, may be misinterpreted with respect to their relevance for large-scale and long-term population dynamics.

Key-words: hymenoptera, natural enemies, population cycles, spatial scale dependence

Introduction

Parasitoids, that is, holometabolous insects (mainly flies and wasps) with parasitic larvae that eventually kill the host, are important enemies of many insects (Godfray 1994). In particular, the action of parasitoids has been highlighted as having a decisive regulatory impact on the cyclic outbreak dynamics of forest defoliating Lepidoptera populations (Berryman 1996; Hassell 2000; Turchin *et al.* 2003). According to the hypothesis of ‘parasitoid-driven outbreak dynamics’, such Lepidoptera populations regularly either escape from the stabilizing effect of direct density-dependent parasitism and/or experience the destabilizing effect of delayed density-dependent parasitism (Hassell 2000). A major tenet of this hypothesis is that parasitism in cyclically outbreaking host populations acts to terminate the outbreaks. Although the importance of larval parasitoids in insects is theoretically well founded and empirically explored in some laboratory systems (Godfray & Shimada 1999; Hassell 2000; Turchin *et al.*

2003), the assumed impact of parasitoids on the dynamics of cyclically outbreaking populations has rarely been empirically demonstrated for natural populations (Myers 1988). Most of the empirical evidence for strong top-down impacts of parasitoids on phytophagous host populations in field studies typically comes from cases of intentionally introduced parasitoids for biological control purposes, often in simple agrosystems (Hawkins *et al.* 1999). In comparison, natural systems can be expected to be more diverse, with complex interactions among many different potentially population-regulating factors that may act to diminish their independent effects (Hawkins *et al.* 1999; Rodriguez & Hawkins 2000; Hunter 2001; Stireman & Singer 2002; Bonsall *et al.* 2004). Consequently, a stronger focus on studying natural parasitoid–host systems is warranted.

The two geometrid moth species *Operophtera brumata* L. (winter moth) and *Epirrita autumnata* Bkh. (autumnal moth) are the major defoliators of sub-arctic birch forest in northern Fennoscandia. Outbreaks, typically extending over 2–3 years sometimes result in forest death and, hence, can have strong ecosystem impacts. As a result of extraordinary long-

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Fig. 1. Larvae of the gregarious ectoparasitoid *Eulophus lavarum* on the carcass of a larval geometrid host (*Operophtera brumata*).

term historical records of outbreak years (dating as far back as the 1860s), showing that both species exhibit large-scale *c.* 10-year outbreak cycles in this geographic region (Tenow 1972; Nilssen, Tenow & Bylund 2007), they have been promoted as prime examples of such cycles (e.g. Berryman 2002; Dwyer, Dushoff & Yee 2004). Recent syntheses of empirical studies, mainly conducted on *E. autumnata* in the continental sections of northern Fennoscandia, have claimed support for the hypothesis that natural enemies underlie the temporal and spatial variations in population dynamics of birch forest geometrids (Ruohomäki *et al.* 2000; Klemola *et al.* 2002; Tanhuanpää *et al.* 2002). Specifically, larval parasitoids (i.e. parasitoids attacking host larvae), which can exhibit very high prevalence rates (80–100%; Bylund 1995; Roland & Embree 1995), have been suspected to be among the most likely mechanisms responsible for the delayed density dependence evident in time-series data (Berryman 1996; Tanhuanpää *et al.* 2002, Fig. 1). However, as outlined in Krebs (1995), population time-series data and discovery of delayed density dependence cannot reveal the mechanism resulting in population regulation (and termination of outbreaks) and mechanistic studies focusing on the demographic effect of the assumed regulatory agent are needed.

The natural first step in the exploration of the role of larval parasitoids in host population dynamics would be to acquire temporal data on the prevalence of parasitism as to test the premise that parasitoid-induced mortality is able to account for the decline in host population growth rate during the

termination of outbreaks. In statistical terms, this means that the level of parasitism in year t ought to exhibit a direct (i.e. non-lagged), negative correlation with host population growth rates between the years t and $t + 1$. Note that this corresponds to a lagged correlation between population densities of moths and parasitism (e.g. Hunter, Varley & Gradwell 1997). Such a correlation, or predictive power of parasitism on geometrid population growth, is a *necessary* condition under the hypothesis of ‘parasitoid-driven outbreak dynamics’. Given confirmatory evidence for this condition based on observational data, further experimental analyses must be conducted to demonstrate whether regulation by larval parasitoids is a *sufficient* condition and therefore unambiguously the cause of outbreak termination.

The approach based on observational data outlined before [coined an ‘accounting approach’ by Korpimäki & Krebs (1996)] has been commonly used to demonstrate that mortality inflicted by specialist predators is a significant predictor of population crashes in several species of cyclically fluctuating small mammals (Korpimäki & Krebs 1996; Korpimäki *et al.* 2004). In the case of natural geometrid populations, however, ‘the accounting approach’ has received little attention. This probably owes to the difficulty of obtaining robust estimates of parasitism rates for all the critical phases (increase, peak and crash) of the 10-year geometrid population cycle (Ruohomäki *et al.* 2000). Consequently, estimates of larval parasitism are mostly obtained from very short-term and small-scale samples [i.e. at the scale of individual trees in, e.g. Bylund (1995) and Virtanen & Neuvonen (1999)]. Opposed to that, moth outbreaks are spatially synchronized at a much larger scale, typically covering habitat at the scale of several square kilometres (Jepsen *et al.* 2009). The validity of results derived from small-scale and short-term parasitoid studies needs thus to be verified at scales relevant to the observed outbreak dynamics.

Here we report from an appropriately scaled observation study of geometrid moth populations in the coastal section of the mountain birch forest in northern Norway with the aim to assess the role of larval parasitoids in moth outbreak cycles according to an accounting approach (Korpimäki & Krebs 1996). In these coastal birch forests, sympatric populations of *E. autumnata* and *O. brumata* with cyclic outbreak dynamics are distributed from sea level to the altitudinal tree line (Tenow 1972; Nilssen *et al.* 2007). The population outbreaks typically differ in magnitude and timing between altitudes and species (Tenow *et al.* 2007; Klemola, Andersson & Ruohomäki 2008). This setting provides scope for including variation in geometrid population dynamics as well as opportunities for estimating parasitism in a relatively short-term study. Thus, in the present 8-year study, we were able to encompass substantial variation in parasitism rates and geometrid outbreak patterns. This facilitated a statistical assessment of the ability of parasitoid-induced moth larval mortality to predict the termination of cyclic moth outbreaks at a spatial scale that matches the observed temporal dynamics. Simultaneously, the particular spatial design of our study also made us able to separately assess the spatial effect of par-

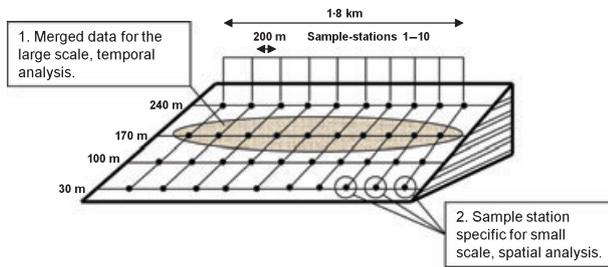


Fig. 2. Schematic illustration of the study design, with data sampling at ten sampling stations along each of four altitude-specific transects, as well as the handling of the data in the two sets of analyses focusing on large-scale temporal effects (1) and small-scale spatial effects (2) of parasitism.

asitoids on a spatial scale similarly small to previous assessment of parasitoid–geometrid moth relations. We used the latter analysis to highlight that an appropriately scaled study design is crucial in the analysis of trophic dynamics involving outbreaking insect populations.

Materials and methods

STUDY SPECIES

Epirrita autumnata and *O. brumata* have a similar univoltine life cycle with non-overlapping generations. Eggs are laid during the autumn on tree trunks and twigs and hatch in spring in concert with budburst, which seems essential for the development of the larvae (Visser & Holleman 2001; Mjaaseth *et al.* 2005). The solitary larvae undergo five instars during 1–1.5 months while feeding on mainly mountain birch in northern Fennoscandia during the early summer until they pupate in the soil. The pupal stage lasts about 2.5 months for *E. autumnata* and about 3 months for *O. brumata* at the environmental and geographical conditions of our study site. Eclosion and mating happen in September for *E. autumnata* and in October for *O. brumata*, respectively. Both moths generally are highly polyphagous, but mainly feed on the dominating pubescent and mountain birch (*Betula pubescens* Ehrh.; *Betula pubescens czerepanovii* Orlova) in northern Fennoscandia.

STUDY DESIGN

The study was carried out within a belt of continuous mature mountain birch forest on the island Reinøya (70°00'N, 19°49'E) in the

coastal district of Troms County in northern Norway (see Mjaaseth *et al.* 2005; Hagen *et al.* 2008 for a detailed description of the study area). Four transects were established at increasing altitude from sea level to the tree line; that is, at 30, 100, 170 and 240 m a.s.l., respectively. Each of the four altitude-specific transect had 10 replicated sampling stations spaced at 200-m intervals (Fig. 2).

The density of larvae (i.e. *E. autumnata* and *O. brumata*) at the 40 sampling stations was estimated during the years 2001–2008 in late June to early July by standard methods, that is, haphazard sampling of 10 equally sized mountain birch branches (length about 60–80 cm), cut *c.* 1–2 m above the ground from different trees in a radius of *c.* 30 m around the sample stations. The branches were carefully shaken in a large plastic box until all larvae had detached and the number of larvae was counted (Hagen, Ims & Yoccoz 2003; Ims, Yoccoz & Hagen 2004; Mjaaseth *et al.* 2005).

Collection of larvae for parasitoid rearing and assessment of parasitism was performed using the same method but at a later stage of larval development (approximately during the fourth instar) to avoid over- or underestimation of parasitism rates (Teder *et al.* 2000). Additionally, to avoid bias owing to phenological differences in larval development across altitudes (Mjaaseth *et al.* 2005), we sampled the transects at slightly different times, starting at 30 m and finishing at 240 m. When moth populations at a given altitude had concluded the crash phase of the cycle, adequate parasitism samples could not be obtained any longer because of extremely low moth larvae abundances. Hence, parasitism sampling was then abandoned for practical reasons, although parasitoids presumably were still prevalent in the low-phase populations. A total of 4282 *E. autumnata* larvae and 11 832 *O. brumata* larvae were collected during the years 2001–2005, only. The number of larvae per year, altitude and species used for estimation of prevalence of parasitism are given in Table 1. Larvae perishing through unknown causes were omitted from these estimates.

According to standard laboratory procedure, the larvae were housed in 1-L 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 within one box to facilitate counting and keeping of the material. Feeding with fresh clipped birch leaves was conducted every third day and emergence of parasitoids as well as unidentified mortality was recorded. When all larvae had either died or pupated, the boxes were stored at a central 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 presence of parasitoids. Eight

Table 1. Means (\pm 95% confidence intervals) of year- and altitude-specific parasitism rates for the two host species during the years 2001–2005. Sample sizes per altitude and year of larvae collected for calculation of parasitism rates are given in parentheses

| | Years | 30 m | 100 m | 170 m | 240 m |
|----------------------------|-------|-----------------------|-----------------------|-----------------------|-----------------------|
| <i>Epirrita autumnata</i> | 2001 | 0.38 \pm 0.20 (24) | 0.19 \pm 0.07 (92) | 0.73 \pm 0.19 (26) | 0.62 \pm 0.18 (60) |
| | 2002 | 0.20 \pm 0.13 (44) | 0.20 \pm 0.11 (80) | 0.56 \pm 0.18 (80) | 0.66 \pm 0.11 (184) |
| | 2003 | 0.20 \pm 0.05 (544) | 0.04 \pm 0.03 (909) | 0.15 \pm 0.06 (420) | 0.06 \pm 0.02 (861) |
| | 2004 | NA | 0.15 \pm 0.06 (117) | 0.41 \pm 0.14 (187) | 0.54 \pm 0.07 (296) |
| | 2005 | 0.53 \pm 0.15 (59) | 0.46 \pm 0.16 (63) | 0.74 \pm 0.22 (19) | 0.74 \pm 0.24 (54) |
| <i>Oporophtera brumata</i> | 2001 | 0.53 \pm 0.06 (668) | 0.17 \pm 0.07 (674) | 0.49 \pm 0.07 (668) | 0.28 \pm 0.09 (337) |
| | 2002 | 0.47 \pm 0.10 (395) | 0.42 \pm 0.08 (849) | 0.66 \pm 0.09 (426) | 0.53 \pm 0.10 (315) |
| | 2003 | 0.35 \pm 0.05 (989) | 0.24 \pm 0.08 (497) | 0.36 \pm 0.11 (817) | 0.19 \pm 0.08 (805) |
| | 2004 | NA | 0.42 \pm 0.15 (165) | 0.43 \pm 0.08 (721) | 0.46 \pm 0.05 (781) |
| | 2005 | 0.33 \pm 0.06 (306) | 0.32 \pm 0.08 (280) | 0.62 \pm 0.09 (474) | 0.36 \pm 0.09 (648) |

NA, not applicable.

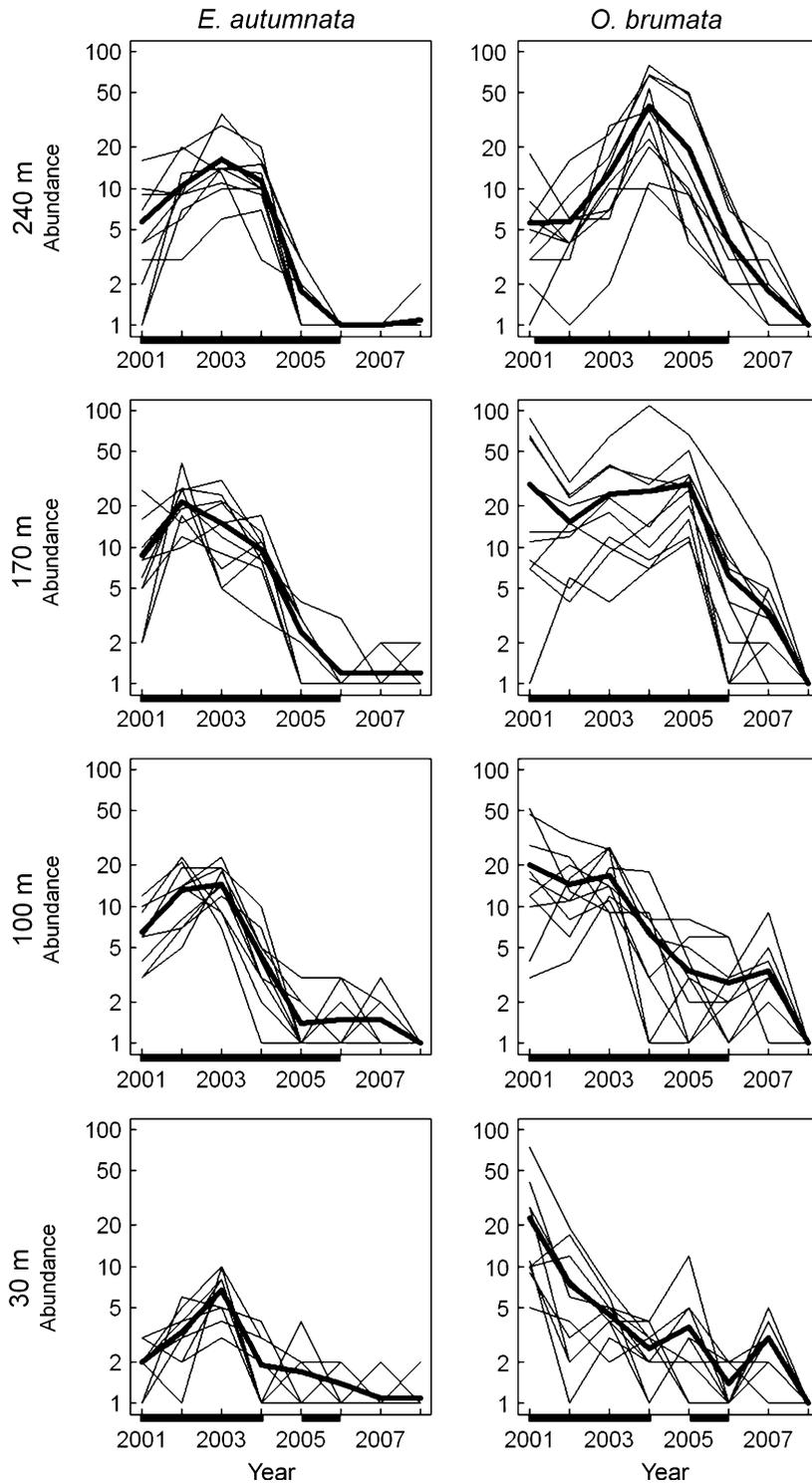


Fig. 3. Altitude-specific population dynamics for the two moth species on a log-scale. Thin curves represent sample-station-specific population densities (based on counts of larvae on 10 haphazardly selected birch branches), whereas thick curves represent altitude-specific means (i.e. average density for the 10 sampling stations per altitude). Bold sections of the x -axes denote the time period for which geometrid growth rates could be analysed for the large-scale temporal impact of larval parasitism.

different species (or species groups) of hymenoptera were identified in each host species of which the numerically dominant one (*Phobocambe* sp./*Sinophorous crassifemur*) was shared by the two host species (Schott 2007).

DATA ANALYSIS

Geometrid population growth rate (R_t), which is the focal response variable in our analyses, was taken as $\log [N_{t+1}/N_t]$, where N_t is the

larval abundance of a given species (*E. autumnata* or *O. brumata*) in year t . As both species have non-overlapping generation life cycles, larval abundance suits well for representing population density. Two sets of analyses highlighting different aspects of parasitoid impacts on geometrid dynamics were conducted.

Our first objective was to examine parasitoid-induced mortality (i.e. proportion of larvae parasitized) as a potential determinant of the distinct species- and altitude-specific temporal dynamics of the two geometrid species (Fig. 3; Hagen *et al.* 2008). Large variation in

larval density (Fig. 3) sometimes resulted in small parasitism sample sizes per sample station (in particular for *E. autumnata*, Table 1). To ensure large sample sizes for robust estimation of both population growth and parasitism rates, data of the 10 sampling stations per altitudinal transects were each merged for species and year (Fig. 2). This handling of the data resulted in one data point for parasitism and moth growth for each year, altitude and species (Table 1). As the station-specific growth rates were highly synchronized within altitudes, this data treatment is justifiable for an analysis of temporal moth dynamics (Hagen *et al.* 2008). Linear models (Gelman & Hill 2007) with the response R_t (growth rate between years t and $t + 1$) and the predictors 'parasitism rate' (in year t , transformed by empirical logit; Cox & Snell 1989) and 'altitude' (categorical variable) were fitted to these species- and altitude-specific data. Note, that we did not include 'year' as a predictor in this analysis as we aimed to assess to which degree parasitism alone could predict the altitude-specific temporal moth population dynamics.

Secondly, we applied linear models for analysing growth rates at the level of sampling stations (Fig. 2). This was performed to test whether parasitism could significantly account for some of the small-scale spatial variance in moth growth rate within the altitudinal transects. As samples for estimates of parasitism on the scale of sampling stations in some years were too small to ensure robust analysis at this level (see before), we used a subset of 3 years (i.e. 2002–2004) with the highest sample sizes for both geometrid species. Rates of population growth and parasitism were estimated as described before, but with a constant = 1 added to counts of geometrid larvae and a constant = 0.5 to the counts of parasitoids to avoid zero entries in the log-ratios and logits of growth and parasitism rates, respectively. To consider the spatial component in the analyses, we included 'year' (categorical variable) and the 'year \times altitude' interaction as predictor terms in addition to the predictors 'parasitism' and 'altitude' from the first set of analyses. Thus, this analysis targets the contribution of parasitism to the spatial variance around the mean year-, species- and altitude-specific growth rates (Fig. 3). As residual spatial autocorrelation in the station-specific growth rate potentially could compromise the reliability of this analysis, the extent of such spatial autocorrelation was investigated using Moran's I on residuals [defined using the nearest eight neighbours (five or three for stations on the edge)]. There was no evidence of strong residual spatial autocorrelation based on Moran's I (*E. autumnata*: all years: $I = -0.0046$, $P = 0.34$; 2002: $I = -0.0071$, $P = 0.30$; 2003: $I = 0.071$, $P = 0.049$; 2004: $I = -0.017$, $P = 0.35$; *O. brumata*: all years: $I = 0.013$, $P = 0.062$; 2002: $I = 0.058$, $P = 0.058$; 2003: $I = 0.0077$, $P = 0.22$; 2004: $I = -0.093$, $P = 0.71$). Nevertheless, we also estimated the effect size of spatial variation in parasitism using

mixed effect models with year as random effects adjusted for spatially autocorrelated errors (Pinheiro & Bates 2000). In these models, we investigated different forms for the relationship between correlation and distance (linear, spherical and exponential) as the correlograms were flat and did not point to a specific model. The results were very similar and we only present the results from models with spherical autocorrelation. Temporal autocorrelation was checked for by fitting mixed effect models with sampling stations as random effects and with first-order temporal autocovariance (AR1) in the residuals.

Model selection (of fixed terms) in all analysis was based on minimizing Akaike information criterion (AIC; Burnham & Anderson 2002), but retaining the focus variables in the model to estimate the important biological effect. All analyses were performed in R 2.9.1, the models with autocorrelation accounted for being implemented in the libraries SPDEP and NLME.

Results

SPECIES- AND ALTITUDE-SPECIFIC GEOMETRID OUTBREAK DYNAMICS

The cyclic phases of late increase, peak and crash were well represented in the time series of both geometrid species (Fig. 3). However, the timing of these phases differed both between altitudes and species. There was distinct dynamical asynchrony between the altitudes in *O. brumata* owing to more delayed peaks and steeper crashes at higher than lower altitudes (Fig. 3). The dynamic of *E. autumnata* was generally more synchronous, but with a tendency for lower peak abundances at the lowest altitude. The timing of the peaks, as well as the onsets and terminations of the crash phase, did not coincide for the two geometrid species at any altitude (Fig. 3). At none of the altitudes was the outbreak density of larvae high enough to cause significant defoliation of the birch forest.

LARGE-SCALE TEMPORAL EFFECT OF PARASITISM

The rate of parasitism was clearly patterned among years and altitudes in both geometrids (Table 1). However, although the rates ranged widely at the transect level (4–74% in *E. autumnata* and 17–66% in *O. brumata*), the temporal variation in host population growth appeared not to be related to cor-

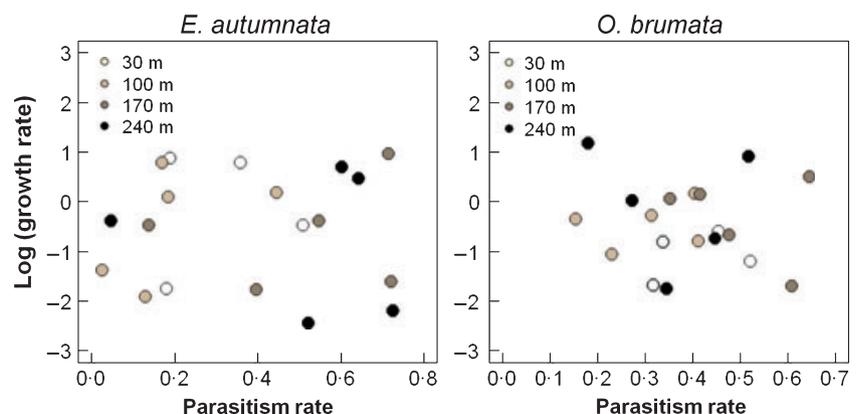


Fig. 4. Scatter plots of altitude- and species-specific geometrid growth rates against corresponding rates of parasitism rates (see Table 1). Different altitudes are indicated with differently shaded dots.

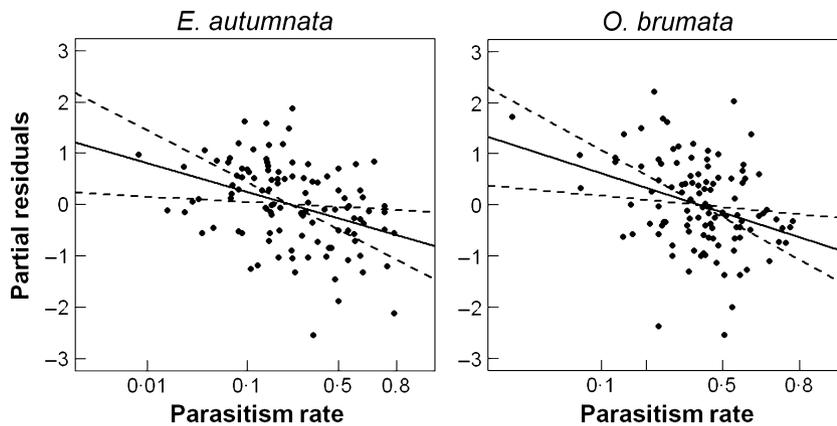


Fig. 5. Small-scale spatial effects of larval parasitism on geometrid growth rates. The plots are based on partial residuals from the linear models of local station-specific growth rates corrected for the effect of year and altitude. Note that the x-axis is back-transformed from logit to proportion. Solid lines depict the estimated effect of parasitoids; dashed lines represent confidence intervals of the slope.

responding variation in larval parasitism at any altitude (Fig. 4). This was confirmed by the statistical modelling of geometrid population growth rate. According to AIC, both altitude (*E. autumnata*: AIC = 69.58; *O. brumata*: AIC = 54.39) and the parasitism \times altitude interaction (*E. autumnata*: AIC = 74.00; *O. brumata*: AIC = 59.39) could be dropped from these models (*E. autumnata*: AIC = 64.68; *O. brumata*: AIC = 52.17). This left non-significant and minute effects of parasitoids [i.e. slope estimate ($b \pm 95\%$ confidence intervals) of the estimated relation between parasitism and the logit-transformed moth growth rate] amounting to $b = 0.04 \pm 0.48$ ($R^2 = 0.002$, $P = 0.86$, d.f. = 17) in *E. autumnata* and $b = -0.15 \pm 0.72$ ($R^2 = 0.01$, $P = 0.67$, d.f. = 17) in *O. brumata*. A model based on growth rate in both species jointly gave the parameter estimate $b = 0.008 \pm 0.35$ ($R^2 = 0.0001$, $P = 0.96$, d.f. = 36).

SMALL-SCALE SPATIAL EFFECTS OF PARASITISM

When judged from the sampling station-specific population trajectories (Fig. 3), it was found that there was clearly more spatial population dynamic variability within altitudes in *O. brumata* than in *E. autumnata*. In the general linear models of local (i.e. sampling station-specific) growth rates, corrected for the effect of year and altitude, the local rates of parasitism accounted for some of the spatial variation in moth growth rate (Fig. 5, partial $R^2 = 0.11$, $P = 0.02$, d.f. = 103 for *E. autumnata* and partial $R^2 = 0.12$, $P = 0.007$, d.f. = 103 for *O. brumata*). The estimated negative effects [i.e. the slope (b) of the logit parasitoid–moth growth rate relation] were almost identical between the simple linear fixed effects model and the mixed effect model accounting for spherical spatial autocorrelation (results from model with autocorrelation: *E. autumnata*: $b = -0.223$ with SE = 0.094 compared with -0.233 , SE = 0.095 for the linear model without autocorrelation; *O. brumata*: $b = -0.326$, SE = 0.124 compared with -0.349 , SE = 0.126). The estimated range of the autocorrelation for the two moth species was less than the distance between two neighbouring stations (*E. autumnata*: 100.3 m, *O. brumata*: 84 m). Models considering temporal autocorrelation (sampling stations as random effects and AR1 structure in the residuals) gave a somewhat smaller effect of parasitism, however, still significant for *O. brumata* (*O. bru-*

mata: $b = -0.272$, SE = 0.111, $P = 0.0170$ and *E. autumnata*: $b = -0.148$, SE = 0.089, $P = 0.103$).

Discussion

As parasitoid-inflicted larval mortality did not account for the distinctly altitude- and species-specific patterned geometrid outbreak dynamics in our study, no support was found for the hypothesis that larval parasitoids terminated the outbreaks at the spatial scale; these outbreaks are observed in coastal mountain birch forests in northern Fennoscandia. The only discernible effect of larval parasitism was a modest contribution to the variability around the mean altitude- and year-specific dynamics. Thus, this spatial effect of parasitoids (i.e. contribution to local variability), possibly because of aggregative behaviour of mobile wasps, may have acted to counteract cyclicity and spatial synchrony rather than the opposite (Hassell 2000). Hunter *et al.* (1997) similarly found that different factors affected the spatial vs. temporal variance in the dynamics of winter moths in England.

Inferences about the role of parasitoids on insect populations (and more generally the role of natural enemies in population dynamics) can be derived from different research approaches having their own strengths and weaknesses (Hunter 2001). Here, we adopted what has been termed an ‘accounting approach’ in studies of the role of predation in population cycles of herbivorous small mammals (Korpimäki & Krebs 1996). In this approach, which bears many similarities to the early life table studies on geometrid populations (e.g. Varley, Gradwell & Hassell 1973), the first step is to obtain robust estimates of enemy-inflicted mortality over the different phases of the population cycle. The relatively few estimates obtained for cyclic forest Lepidoptera show that parasitism rate can be temporally high (Berryman 1996). This has led several investigators, including ourselves, to consider larval parasitism as potentially important in the termination of geometrid outbreaks. However, further evidence than infliction of high mortality rates, only, is needed to determine the role of parasitoids (Myers 1996).

The natural next step in the accounting approach is to test if parasitoid-inflicted mortality actually predicts host population rate of change. Given that a confirmatory result is obtained (e.g. Morris 1959), the causality behind any signifi-

cant correlation needs to be verified by other research approaches (Hunter 2001; Krebs 2002; Turchin 2003). However, when mortality inflicted by a natural enemy has no predictive power at all, such as in this study, the accounting approach can be a very efficient means of eliminating natural enemies from further enquiry. Obviously, lack of predictive power can be expected in cases when enemy-inflicted mortality rates are invariably low. It is more unexpected when the rates range as widely as they did in our study (e.g. 4–74% in *E. autumnata*). However, in that case the presence of strongly compensatory mechanisms acting on the host populations may override the effect of single mortality factors. Indeed, the difference in the strength of top-down impacts of parasitoids between simple agrosystems and complex natural food webs of forest ecosystems (Hawkins *et al.* 1999) may originate from different prevalence of compensatory mechanisms.

The main obstacle for studying the role of parasitism in cyclically outbreaking populations of geometrids is the demanding efforts in field and lab work required to obtain robust estimates of parasitism rates for different phases of the cycle (Ruohomäki *et al.* 2000). The only other relevant study of mountain birch forest geometrids we are aware of is the one reported in Bylund (1995). Also in that study, conducted on *E. autumnata* in continental mountain birch forest, larval parasitism (although temporally very high) failed to predict population rate of change. Nevertheless, owing to the occasionally high rate of parasitism, Berryman (1996) included *E. autumnata* (as well as *O. brumata*) on his list of outbreaking forest Lepidoptera with larval parasitoids as the most likely regulating mechanism. Moreover, Tanhuanpää *et al.* (2002) used the fact that the parasitism reported in Bylund (1995) was delayed density dependent in a simulation model and concluded that larval parasitism by itself could explain the cyclic outbreak dynamics in *E. autumnata*. However, as pointed out by others (Liebhold & Kamata 2000; Ruohomäki *et al.* 2000; Hunter 2001) delayed density dependence by itself cannot be used to verify cause and effect relations in the dynamics of outbreaking Lepidoptera populations. Thus, we conclude that there appears to be no empirical evidence for the assumed importance of larval parasitoids in terminating outbreaks in cyclic populations of *E. autumnata* and *O. brumata*.

Finally, our study highlights two caveats that are likely to limit the utility of manipulative experiments to unravel the role of natural enemies in Lepidoptera population dynamics. First, owing to the distinctly stage-structured Lepidopteran life cycle, experiments are normally restricted to testing for effects within separate life stages (e.g. mortality within the larval stage; Tanhuanpää, Ruohomäki & Uusipaikka 2001). However, as evident from this study, enemy-inflicted mortality within a life stage in one generation may not impact the abundance of the same life stage in the next generation. Compensatory mechanisms, such as other groups of enemies acting on other life stages, may be the reason for this (Myers 1988). For instance, pupal and egg parasitoids have been reared from other samples of *E. autumnata* (Klemola *et al.* 2009).

Secondly, as experiments typically rely on specific remedies to exclude natural enemies such as netting bags (e.g. Tanhuanpää *et al.* 2001) they rarely exceed the spatial scale of individual host tree and the temporal scale of a year. Thus, experiments and small-scale observational studies tend to emphasize the spatial impacts of enemies at a quite local scale, for which studies in other host–parasitoid systems have demonstrated strong effects (Maron & Harrison 1997). But as exemplified by this study, local spatial effects of larval parasitoids may have no bearing on what is really the focal issue in this case, namely the large-scale outbreak dynamics that characterize sub-arctic birch forest geometrids.

Acknowledgements

The authors thank Tony Christopheit, Simen Pedersen, Einar Stikbakke, Ragnhild Mjaaseth and Ove Sørlibråten for assistance in the field. The constructive comments made by two reviewers both improved the analysis and the presentation of this study. This work was funded by the Department of Arctic and Marine Biology, University of Tromsø, and the Research Council of Norway.

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Received 28 April 2009; accepted 26 January 2010

Handling Editor: Frank van Veen