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Spatially mismatched trophic dynamics: cyclically outbreaking geometrids and their larval parasitoids

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For trophic interactions to generate population cycles and complex spatio-temporal patterns, like travelling waves, the spatial dynamics must be matched across trophic levels. Here, we propose a spatial methodological approach for detecting such spatial match–mismatch and apply it to geometrid moths and their larval parasitoids in northern Norway, where outbreak cycles and travelling waves occur. We found clear evidence of spatial mismatch, suggesting that the spatially patterned moth cycles in this system are probably ruled by trophic interactions involving other agents than larval parasitoids.

Keywords: population cycles; population synchrony; natural enemies; hymenoptera; travelling waves

1. INTRODUCTION

What drives population cycles is a long-standing question still subject to intense enquiries (Ims *et al.* 2008). Recently, to potentially shed new light onto the decisive processes, the ‘spatial dimension’ of population cycles has been emphasized (for reviews, see Liebhold *et al.* 2004; Sherratt & Smith 2008). A host of theoretical studies have deduced how various factors can bring about different spatial patterning of population cycles, from region-wide synchrony to complex patterns of small-scale asynchrony (e.g. Hagen *et al.* 2008). Likewise, many recent empirical analyses based on population time series have shown that the spatial patterns deduced from models are indeed observed in natural populations. Nevertheless, it has proved difficult to pinpoint the mechanisms underlying a given spatio-temporal dynamics based on such population census data alone (Bjørnstad *et al.* 1999; Liebhold *et al.* 2004).

Spatial data on key demographic parameters, in addition to conventional population time series, would allow for stronger tests of hypotheses about processes (Bjørnstad *et al.* 1999; Sherratt & Smith 2008). For instance, natural enemies have often been put forward as a decisive mechanism generating population cycles and distinct forms of spatial population asynchrony (e.g. Bjørnstad *et al.* 2002). In that case, the spatial patterning of enemy-inflicted mortality should

match with the pattern of victim population dynamics. However, Sherratt & Smith’s (2008) review of spatio-temporal dynamics of cyclic populations due to trophic interactions found no examples of such studies. Here, we demonstrate how targeted field studies invoking spatial demographic data can be used to reject specific trophic mechanisms as decisive for the spatio-temporal dynamics of cyclic species, using geometrid moths in northern Fennoscandia as an example.

2. MATERIAL AND METHODS

(a) Study system

Geometrid moths in northern Fennoscandia (i.e. *Operophtera brumata* and *Epirrita autumnata*) have been put forward as prime examples of 9–10 year population cycles likely to be driven by natural enemies (e.g. Berryman 1996; Ruohomäki *et al.* 2000). In particular, observations of locally high larval mortality caused by hymenopteran parasitoids have been used to advocate the hypothesis that larval parasitoids can terminate population outbreaks and thereby generate cyclic dynamics (Berryman 1996; Klemola *et al.* 2002; Tanhuanpää *et al.* 2002). Furthermore, spatio-temporal dynamics compatible with trophic interactions, e.g. travelling waves, a form of spatial asynchrony likely to result from enemy–victim interactions (Sherratt & Smith 2008), have been reported to occur (e.g. Tenow *et al.* 2007).

(b) Methodological approach

Obtaining data on the demographic impact of larval parasitism relevant for analysis of large-scale and long-term spatio-temporal patterns is difficult (Ruohomäki *et al.* 2000), but possible if targeted adequately in time and space. An appropriate timing is the onset of the population cycle’s crash phase, when parasitism should most strongly affect population growth rate, i.e. terminate the outbreak, and high densities allow adequate samples. An appropriate spatial extent (*sensu* Bjørnstad *et al.* 1999) is an area with spatial asynchronous moth dynamics. By combining data on parasitism and moth population change, it can then be tested both whether the spatial patterning of parasitism matches the pattern of asynchrony of moth dynamics, and whether parasitism predicts spatial variation in moth dynamics. Unless both of these conditions are met, parasitism is unlikely to be the causal mechanism behind the large-scale outbreak cycles: if only the first condition is met, the parasitoids track the host populations without affecting their dynamics. If only the second condition is met, the parasitoids only affect the host dynamics locally.

Since 1999, we have monitored geometrid population dynamics in subarctic Norway. In 2005, an opportunity arose at one locality (figure 1a) to implement the empirical approach described above during the crash phase of the outbreak cycle (figure 2a). Based on previous reports (e.g. Tenow *et al.* 2007), describing spatial asynchronous dynamics compatible with travelling waves, we expected the populations to crash asynchronously along an inland-coast gradient after 2005. To capture this event, we set up a 70 km transect of 15 regularly spaced sampling sites extending from our long-term monitoring site into the bottom of the fiord (figure 1a).

At each site in late June 2005–2007, larval density was estimated at two adjacent locations in the slope lining the fiord at 30 and 100 m altitudes, respectively, using standard methodology (Ims *et al.* 2004) based on counting the larvae on 10 haphazardly collected birch branches. Sampling for parasitoids followed a similar procedure a week later, approximately during the fourth larval instar. The two samples per site were lumped, which did not affect the results in any way (data not shown), to obtain robust estimates of site specific parasitism. Sample size depended on larval density and sampling was abandoned when the populations had concluded the crash phase due to extremely low densities. Only the year 2005 gave samples with adequate spatial coverage for the purpose of our analysis. The material for this year composed of 1368 *O. brumata* larvae (3–312 per site) and 242 *E. autumnata* larvae (3–28 per site) that were available for the laboratory procedures to estimate rate of parasitism (see Hagen *et al.* 2006 for details of laboratory procedures).

(c) Data analysis

Geometrid population growth was taken as $R_t = \log[(N_{t+1} + 1)/(N_t + 1)]$, where N_t is larval number per site in year t . Parasitism was taken as $P_t = N_{p,t}/N_{tot,t}$, where $N_{p,t}$ is the number of parasitized larvae and $N_{tot,t}$ is the number of cultured larva from a site. In all statistical analyses $t = \text{year } 2005$. Spatial match–mismatch between moth dynamics (i.e. R_t) and parasitism (P_t) was examined using standard methods (Bjørnstad *et al.* 1999) based on graphically assessing whether the spatial autocorrelation

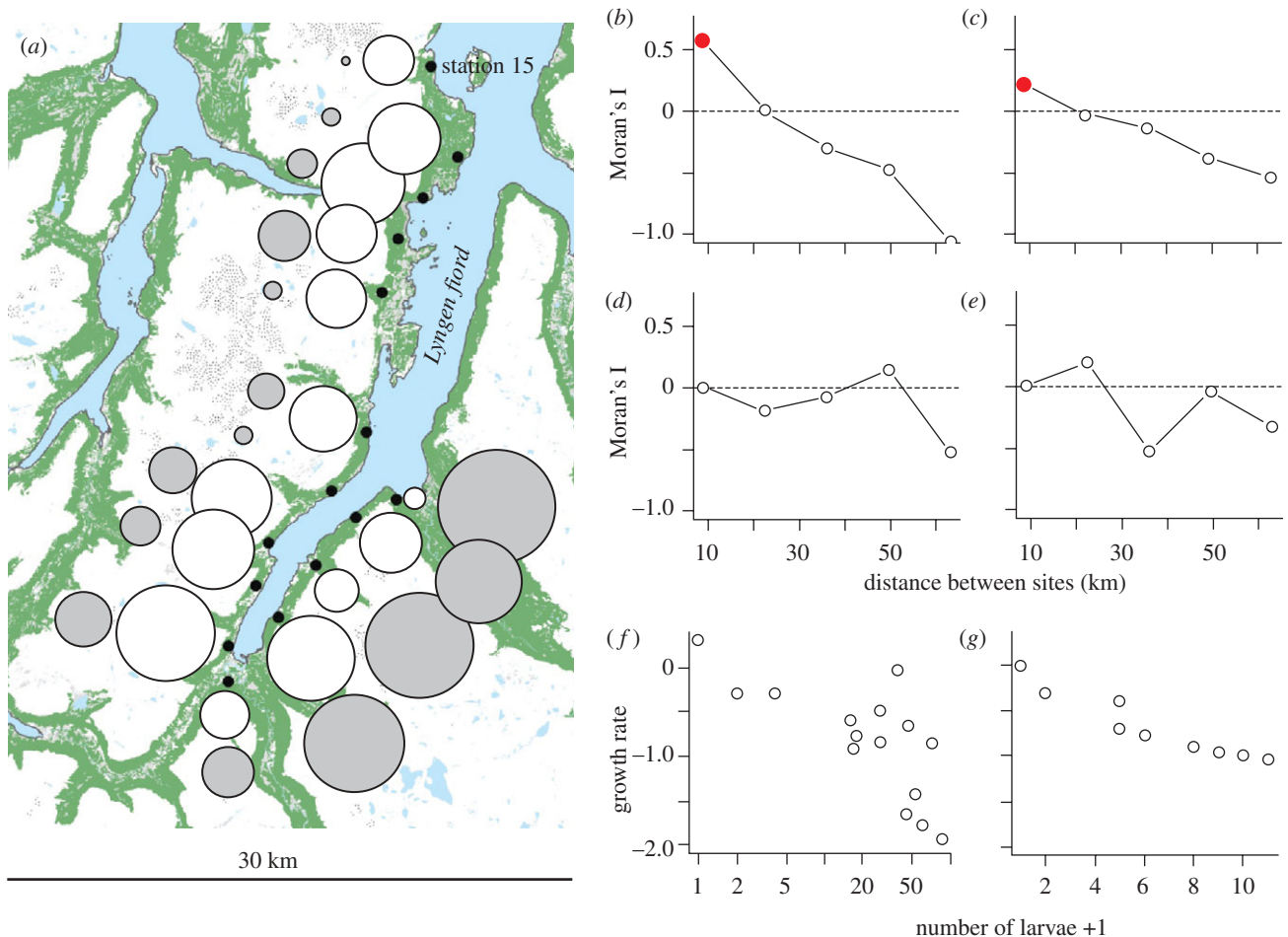


Figure 1. (a) The location of the 15 sampling sites (black filled circles). Sizes of circles are proportional to magnitude of population crash rates (grey filled circle) and parasitism rates (white filled circle) of *O. brumata* at each site. (b,c,d,e) Spatial autocorrelation (i.e. Moran's I, which can be interpreted as an ordinary correlation coefficient) in (b,c) population crash rate and (d,e) in parasitism rate among sites with increasing overland distance. Red filled circles indicate significant autocorrelation ($p < 0.05$), i.e. none of the negative values are significant. (f,g) Population crash rate versus larval density. (b,d,f) *O. brumata*; (c,e,g) *E. autumnata*.

profiles (correlograms) for moth dynamics were consistent with the equivalent profiles of the parasitoid prevalence rates. The correlograms were constructed based on Moran I statistics (Moran 1950), which can be interpreted as an ordinary correlation coefficient, and shows the degree of spatial synchrony (or correlation) based on significance testing of distance-specific autocorrelations (Bjørnstad *et al.* 1999). Distance between transect sites was taken as the shortest over-land distance, as even short stretches of unsuitable habitat may affect the spatial dynamics of this system (Ims *et al.* 2004). The local impact of parasitism on population rate of change was quantified by linear regression with R_t as the response variable and P_t as the predictor variable.

3. RESULTS

As anticipated when designing the study, the moth populations crashed during the next two years (figure 2a–c). Most of the *E. autumnata* populations had already crashed in 2006. The *O. brumata* crash, starting from somewhat higher densities, showed more variation and continued until 2007 at most sites. The crash rate was strongly spatially density-dependent in both species (figure 1f,g).

Moran's I correlograms, based on variation in crash rate along the transect, depicted monotonically declining synchrony with increasing inter-site distance for both moth species, with a steeper cline for *O. brumata*

than *E. autumnata* (figure 1b,c). Thus, the local populations crashed with variable rates that were distinctly spatially structured. The monotonically decaying autocorrelation implies that the crash rates became gradually more dissimilar towards the opposite ends of the transect. Specifically, the inner sites of the fiord crashed more steeply than the outer sites (figure 1a). Significant positive autocorrelation was evident only at inter-site distances up to 10 km (figure 1b,c).

Both the mean and the variance of the site-specific parasitism showed similar, high levels for the two moth species (*O. brumata*: mean $P_t = 34.0\%$, s.d. = 10.2%; *E. autumnata*: mean $P_t = 38.8\%$, s.d. = 18.9%). Overdispersion from random binomial variance in the site-specific parasitism rates (residual deviance/d.f.-ratios for *E. autumnata*: 2.69, $p = 0.007$; *O. brumata*: 4.11, $p < 0.001$) implied significant aggregation of parasitoids along the transect. However, both predictions regarding a regulatory impact of larval parasitoids on moth dynamics were rejected. Firstly, the Moran I correlograms of parasitism (figure 1d,e) did not visually match the correlograms of moth dynamics (figure 1b,c). Parasitism showed no consistent spatial structuring and autocorrelation was not statistically significant at

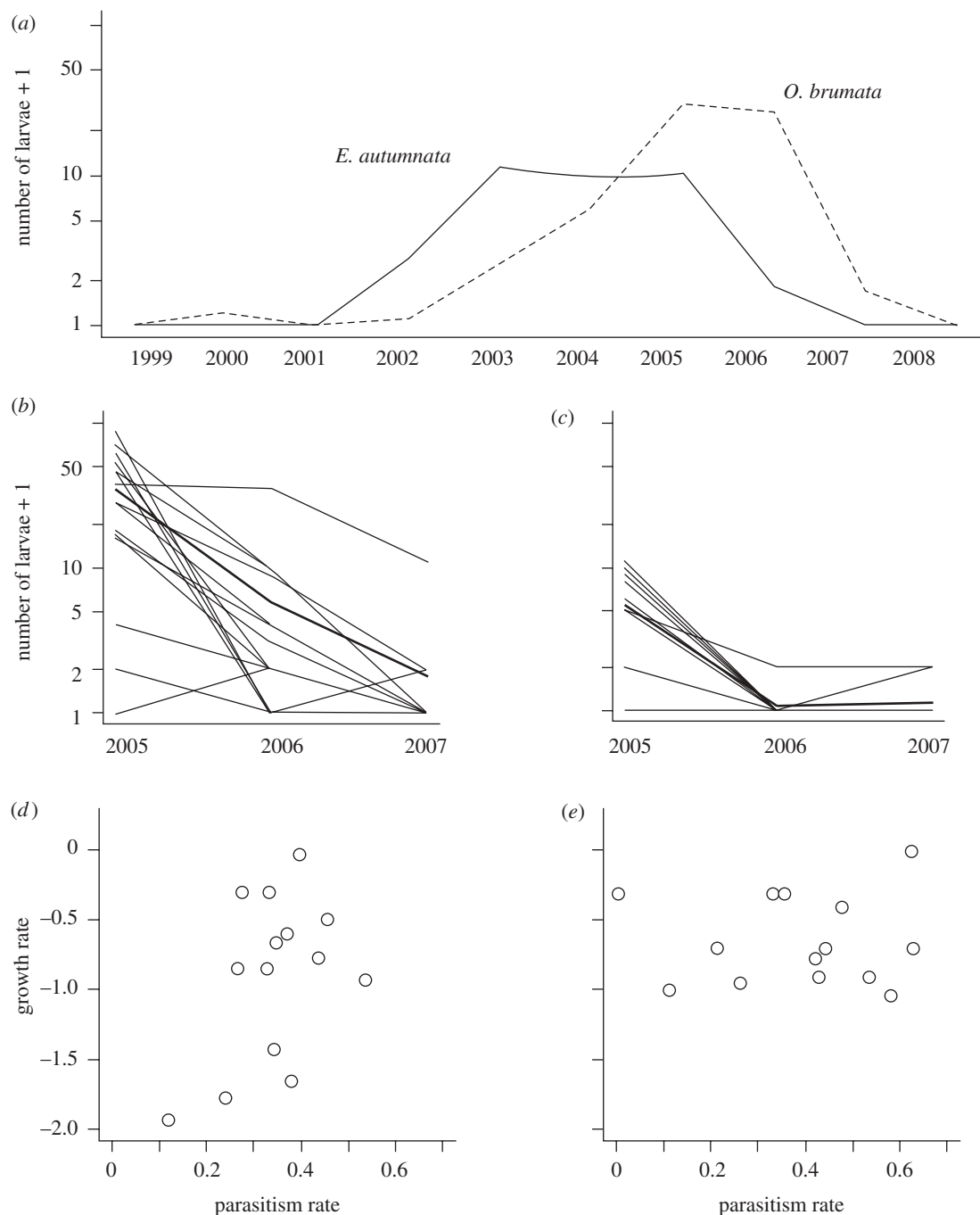


Figure 2. (a) Long-term geometrid population dynamics around sample station 15. (b,c) Population trajectories at the 15 sampling sites (average trajectory in bold). (b, *O. brumata*; c, *E. autumnata*). (d,e) Population growth rate versus parasitism (d, *O. brumata*; e, *E. autumnata*).

any spatial scale (figure 1d,e). Secondly, parasitism did not predict the population crash rate at the site level in either of the moth species (*E. autumnata*: $R^2 = 0.00044$, $p = 0.94$; *O. brumata*: $R^2 = 0.21$; $p = 0.10$; figure 2d,e).

4. DISCUSSION

Our study was specifically targeted to test the proposed decisive role of natural enemies in shaping the large-scale spatial dynamics of cyclic prey populations. Previous empirical studies aimed to highlight spatial aspects of enemy–prey interactions have mostly been conducted on much smaller spatial scales and/or with less spatial replication. An exception is the study

of Satake *et al.* (2004), who estimated the spatial dimension of a pulsed trophic cascade resulting from regional-scale fruit masts in rowan trees, which was propagated bottom-up to populations of fruit moths and their parasitoids. They found that the spatial correlogram of the parasitoids generally matched that of the moth, but parasitism appeared to have little impact on local moth dynamics.

Prior to the present study, we are not aware of equivalent empirical analyses applied to assess the link between spatial population dynamics and enemy inflicted mortality in cyclic species, although similar analyses do exist from other systems (e.g. Steffan-Dewenter & Schiele 2008). Usually the only spatial data available for cyclic systems are panels of

population time series of the victim population. This also regards previous studies of population dynamics of the two focal geometrid species (e.g. Ims *et al.* 2004; Klemola *et al.* 2006; Tenow *et al.* 2007). Previous studies of impact of parasitoids in these moths have invariably been conducted on relatively small spatial scales, and even such local studies have not proved that larval parasitoids are able to terminate outbreaks (Ruohomäki *et al.* 2000). The assumed importance of larval parasitoids appears mostly to be derived from the high mortality rates they have been reported to inflict locally or temporally (Berryman 1996). Such high rates were also seen, at least locally, in our study. However, they were not able to explain the distinct spatially patterned crashes in the two geometrid moth species.

Thus, we conclude that trophic interactions involving agents other than larval parasitoids are likely to underlie both local density-dependent growth and large-scale population dynamics in these northern birch forest geometrids. We propose that spatial study designs similar to what we have employed here can be specifically targeted to study interactions between moths and their host plant (i.e. mountain birch) and the effect of enemies acting on other moth life stages.

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