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Anisotropic patterned population synchrony in climatic gradients indicates nonlinear climatic forcing

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Although climatic forcing has been suspected to be the most common cause of spatial population synchrony owing to the Moran effect, it has proved difficult to disentangle the impact of climate from other possible causes of synchrony based on population survey data. Nonlinear population responses to climatic variation may be a part of this difficulty, but they can also provide an opportunity to highlight the climate impacts through targeted survey designs. In particular, when species distribution ranges encompass consistent spatial gradients in climate (e.g. according to latitude or altitude), such gradients can be strategically included in the spatial design of population surveys as to facilitate comparisons of spatial synchrony patterns across and along the gradient. In that case, we predict that nonlinear impacts of climatic variation on population growth rates will result in anisotropic (direction specific) synchrony patterns in the sense that synchrony will drop faster with distance along the climatic gradient than across it. We provide an empirical case study to exemplify survey design and analyses. Of two sympatric species of geometrids, inhabiting an altitudinal gradient in subarctic birch forest, one (*Operophtera brumata* L.) showed anisotropic synchrony consistent with a strongly nonlinear sensitivity to climatic variation, whereas the other (*Epirrita autumnata* Bkh.) did not. These results are interpreted in light of the biological characteristics of the species.

Keywords: altitude; correlogram; forest insects; Moran effect; population outbreaks

1. INTRODUCTION

Population ecology is increasingly focused on spatial (geographical) dynamics (Bascompte & Solé 1998; Bjørnstad *et al.* 1999; Lundberg *et al.* 2000; Klemola *et al.* 2002). In particular, many recent studies have investigated population synchrony, i.e. the strength and scale of spatial covariance in population dynamics (Bjørnstad *et al.* 1999). From these studies, synchrony seems to be taxonomically and geographically widespread (Hudson & Cattadori 1999; Koenig 1999). However, importantly there is often large variation in the strength of local synchrony and how fast it drops with distance (Ranta *et al.* 1997; Kaitala & Ranta 1998; Kendall *et al.* 2000). Such sources of variation in population synchrony can provide important clues to what are the underlying mechanisms of both synchronization and more generally population dynamics.

Broadly, population synchrony can be caused either by (i) spatially correlated environmental conditions, most notably climate (i.e. the Moran effect) and/or (ii) dispersal, either of the target species or its enemies (Bjørnstad *et al.* 1999; Liebhold *et al.* 2004). The two mechanisms can, to some extent, be expected to produce differently scaled signatures of synchrony (i.e. spatial correlation functions; Bjørnstad *et al.* 1999; Lillegård *et al.* 2005) estimated from population census data in the sense that Moran effect might be more large scale than the effect of dispersal (Ranta *et al.* 1995; Heino *et al.* 1997; Lande *et al.* 1999; Paradis *et al.* 2000). However, in many circumstances, the relative roles of

different synchronizing mechanisms cannot be readily disentangled (Haydon & Steen 1997; Ranta *et al.* 1998; Lande *et al.* 1999; Kendall *et al.* 2000; Abbott 2007), especially when the data stem from the kind of untargeted surveys that usually form the basis for analyses of population synchrony (Bjørnstad *et al.* 1999). On the other hand, stronger inferences can be made from studies that by design are targeted to test specific hypotheses on mechanisms of population synchrony. While randomized and replicated experimental treatments of putative synchronizing mechanisms are impossible in natural populations of most species, there may still be an option to device targeted observational or quasi-experimental studies (Shadish *et al.* 2002) that by design control for dispersal or Moran effects. Previously, such observational studies have controlled for dispersal by including natural (Grenfell *et al.* 1998) or artificial dispersal barriers (Ims & Andreassen 2000) in the design. In this study, we propose to include a spatial gradient in climate as a design measure in population surveys to highlight the nonlinear climate forcing on population dynamics.

Our case study focuses on the two geometrid moth species *Epirrita autumnata* and *Operophtera brumata*, which are renowned for their pronounced cyclic outbreak dynamics in the mountain birch forest in the northern Fennoscandia (Tenow 1972, 1996; Haukioja *et al.* 1988; Hogstad 1997; Ruohomäki *et al.* 2000; Klemola *et al.* 2002; Tanhuanpää *et al.* 2002). Although population outbreaks (in particular in *E. autumnata*) have been claimed to be sufficiently large scale so as to be most compatible with a regionalized Moran effect (Tenow 1972; Berryman 1996;

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Ruohomäki *et al.* 2000; Klemola *et al.* 2006), recent studies have pointed to more complex spatial patterns (Klemola *et al.* 2006; Nilssen *et al.* 2007) and small-scale heterogeneities in the spatial dynamics (Ims *et al.* 2004; Tenow *et al.* 2007) leaving the decisive mechanisms more uncertain.

When addressing Moran effects, the fact that insect life cycles are composed of life stages with typically nonlinear sensitivities to climate parameters requires particular attention. For instance, in the two focal birch forest geometrids, overwintering eggs are killed when winter temperatures become lower than a specific threshold (below approx. -35°C in *O. brumata* and -36°C in *E. autumnata*; Macphee 1967; Tenow & Nilssen 1990). Another candidate for strong nonlinear effects is temperature-dependent phenological matching between insect life stages and their trophic interactants (food plants or enemies; Stenseth & Myserud 2002; van Asch & Visser 2007). Considering the fact that temperature drops consistently with increasing altitude (Körner 2007), such nonlinear demographic responses to temperature variation can be predicted to cause anisotropic (i.e. spatially heterogeneous) population synchrony patterns (Bjørnstad *et al.* 1999) over climatic gradients, i.e. according to altitude or latitude (see figure 1 for a graphical demonstration). Specifically, population synchrony can be expected to be more spatially extensive within than between altitudes and latitudes. Thus, studies on spatial population dynamics invoking altitude or latitude as a design variable, which we exemplify in this study, can provide a means for identifying the action of nonlinear demographic responses to temperature variation.

2. MATERIAL AND METHODS

(a) Study area, design and sampling

The study was conducted in 2001–2007 at Reinøya in northern Norway ($70^{\circ}00'$ N, $19^{\circ}49'$ E) in a north–northeast-oriented slope (mean slope 23.3°) where the mountain birch forest forms a fairly homogenous belt from the sea level and up to the forest limit at approximately 240–250 m elevation. Ten parallel altitudinal transects spaced at 200 m intervals were established. Each transect had four stations at the altitudes of 30, 100, 170 and 240 m. Owing to variation in the steepness of the slope, the length of transects varied between 514 and 628 m and the distance between adjacent transect stations ranged from 84 to 360 m. The orientation (compass direction) of transects was determined by the topography of the north–northeast-oriented slope. The mean orientation of vectors running in the two cardinal directions (i.e. parallel and perpendicular to the altitudinal transects) was estimated from directional vectors drawn towards north and east between adjacent transect stations. The mean orientation along the altitudinal transects was 18.2° (circular variance = 49.4°). Perpendicular to the altitudinal transects (e.g. within altitudes) the mean orientation was 104.7° (circular variance = 55.4°).

The abundance of *E. autumnata* and *O. brumata* at each of the 40 stations (local populations) was estimated once each year in late June to early July. This was done by shaking 10 arm-length birch twigs, collected haphazardly from 10 different trees, over a large plastic box and then counting the larvae of each species. This census method gives a reliable estimate of local larval density (Hagen *et al.* 2003, 2006; Ims *et al.* 2004; Mjaaseth *et al.* 2005). The biological significance of the altitudinal gradient was verified by Mjaaseth *et al.* (2005), who showed that there is an approximate one week's delay in

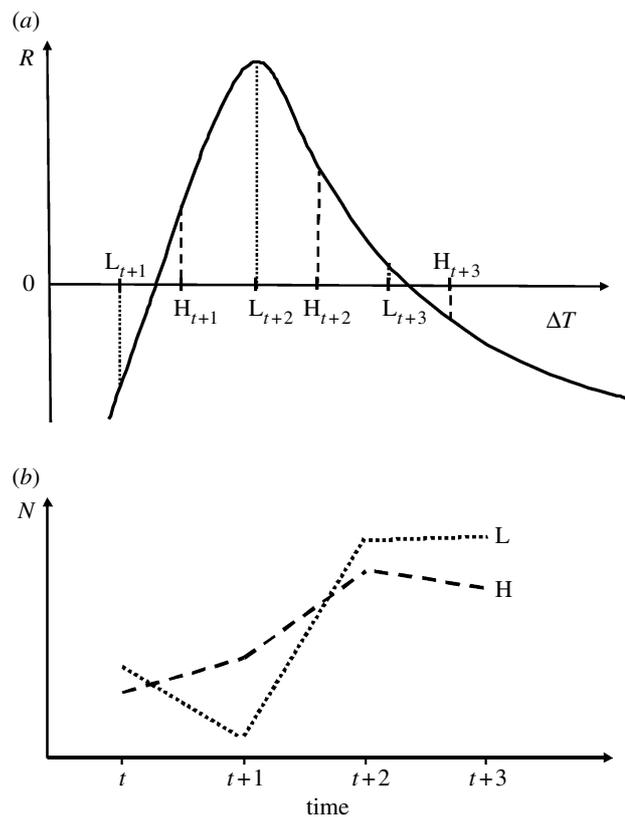


Figure 1. A graphical example of how a nonlinear relationship between insect population growth and a climatic parameter can act to desynchronize population dynamics over an altitudinal gradient. (a) Insect population growth rate (R) as a nonlinear function of a temperature parameter (ΔT). Two insect populations, low (L) and high (H) in an altitudinal gradient are subjected to temporal variation in the temperature parameter over 4 years (from t to $t+3$). The subscript $t+1$ indicate the population growth rate from year t to $t+1$ and so forth. The difference in ΔT between altitudes is assumed to be constant over years, although this is not essential for the argument. (b) Asynchronous dynamics between the low (L) and high (H) altitude populations resulting from the year- and altitude-specific growth rates obtained from (a).

birch budburst and larval development between the lowest and highest elevations. On the other hand, winter temperatures never drop below -20°C in the study area, thus eliminating temperature-dependent egg survival as a determinant of geometrid population dynamics (Mjaaseth *et al.* 2005).

(b) Analytical approach

We used the non-parametric spline correlogram framework of Bjørnstad & Falck (2001) as implemented in the NCF library developed for R (R Core Development Team 2005) for quantifying population synchrony by distance relations. First, we investigated the overall species-specific spatial covariance pattern. This was done by first computing a 'global spline correlogram' for each species based on all population time series, quantifying the degree of spatial synchrony at increasing lag distance, using the function 'Sncf()'. Confidence envelopes for the estimated correlograms were calculated using bootstrapping with 1000 samples (Bjørnstad & Falck 2001). Second, to pinpoint any directional trends in spatial synchrony (anisotropy), and, in particular, whether there was evidence for more spatially extensive synchrony within altitudes than between altitudes, 'directional correlograms' (Bjørnstad *et al.* 2002) were constructed using the

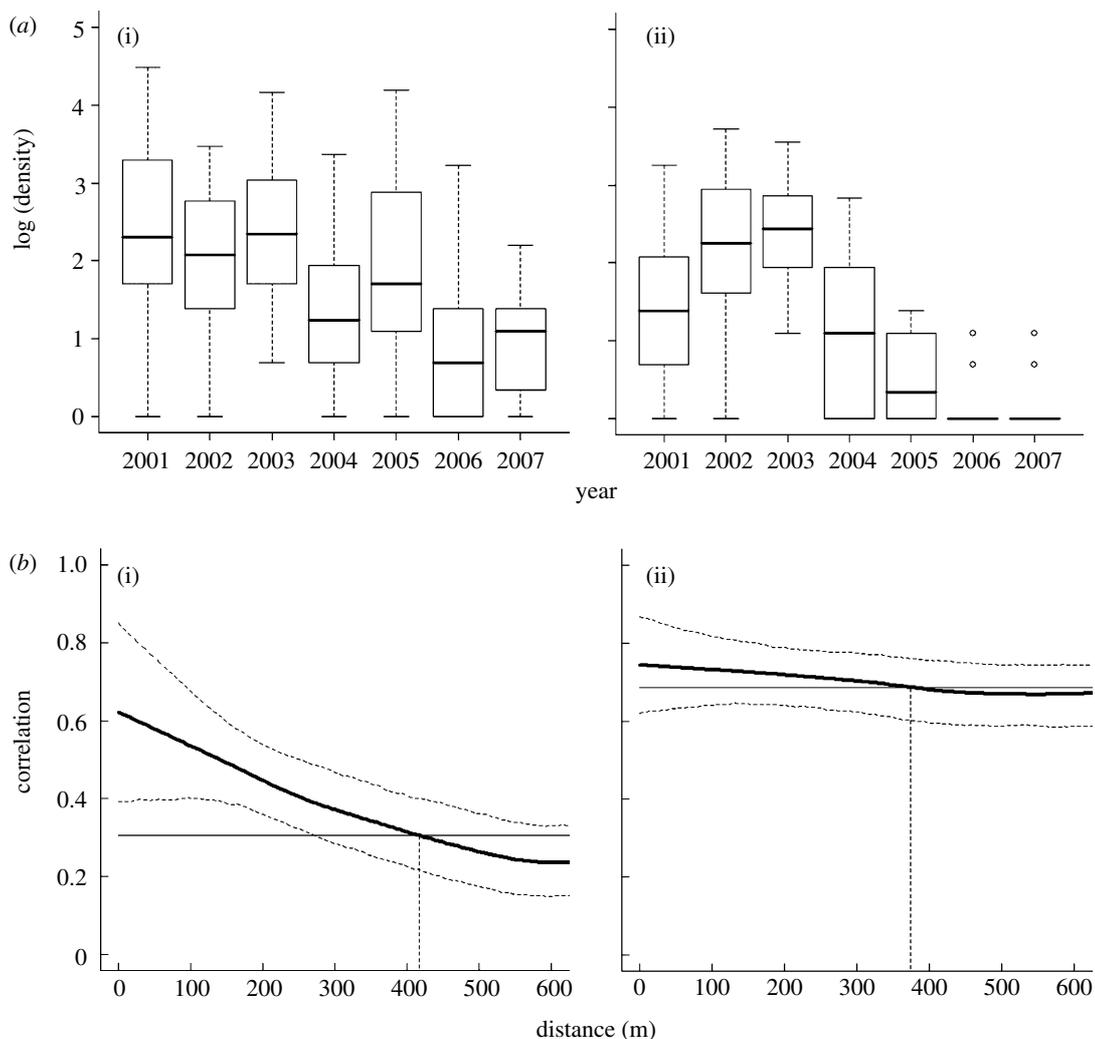


Figure 2. (a) Box plot showing the overall spatial variation and temporal trends across the 40 local time series of population densities of (i) *O. brumata* and (ii) *E. autumnata*. (b) Global spline correlograms (solid lines) with 95% bootstrap confidence envelopes (dashed lines) for both species. The regional average synchrony is indicated by the horizontal solid line (0.31 in *O. brumata*, 0.69 in *E. autumnata*). Local synchrony reached the level of the average regional synchrony at a distance of approximately 400 m in both species (vertical dashed line). However, while distance-specific synchrony is globally indistinguishable from the regional level for *E. autumnata*, population synchrony at short distances is significantly higher than the regional average for *O. brumata*.

function ‘Sncf2D()’ for all compass directions at 3° intervals. A maximum lag distance of 600 m was chosen for all analyses reflecting the approximate straight-line length of the altitudinal transects.

3. RESULTS

The 7-year time series of both species exhibited sufficient temporal variation to provide an useful basis for investigating patterns of population synchrony (figure 2a). That is, all populations had crashed at the end of the study, enabling us to highlight synchrony of the crash phase of the population cycle.

The global (non-directional) spline correlograms depicted quite different spatial synchrony patterns for the two geometrids (figure 2b). *Epirrita autumnata* exhibited strongly synchronous dynamics within the whole spatial extent of the study, and there was only a slight tendency for a decline of synchrony with increasing distance between populations. Most of the local populations of *E. autumnata* went through the stages of late

increase, a sharp peak and a steep crash during the 7-year study period (figure 2a). On the other hand, population synchrony in *O. brumata* was on average lower than in *E. autumnata* and declined distinctly with distance (figure 2b). The local population trajectories showed a great deal of variation, but the overall temporal trend was that the population declines of *O. brumata* was less steep and often lagged behind that of *E. autumnata* (figure 2a).

Inspecting the spatio-temporal dynamics of *O. brumata*, both in terms of directional correlograms (figure 3) and as spatial plots of year-specific local population densities (figure 4), revealed that much of the variation in local dynamics and the overall declining synchrony with distance shown in the global correlogram (figure 2b) could be ascribed to asynchrony between the different altitudes. The directional correlograms (figure 3a,b) showed that synchrony was high between all populations at the same altitude but declined steeply with distance between altitudes. As could be expected from the uniformly high spatial synchrony in *E. autumnata* evident from the global correlogram (figure 2b), there was not much difference

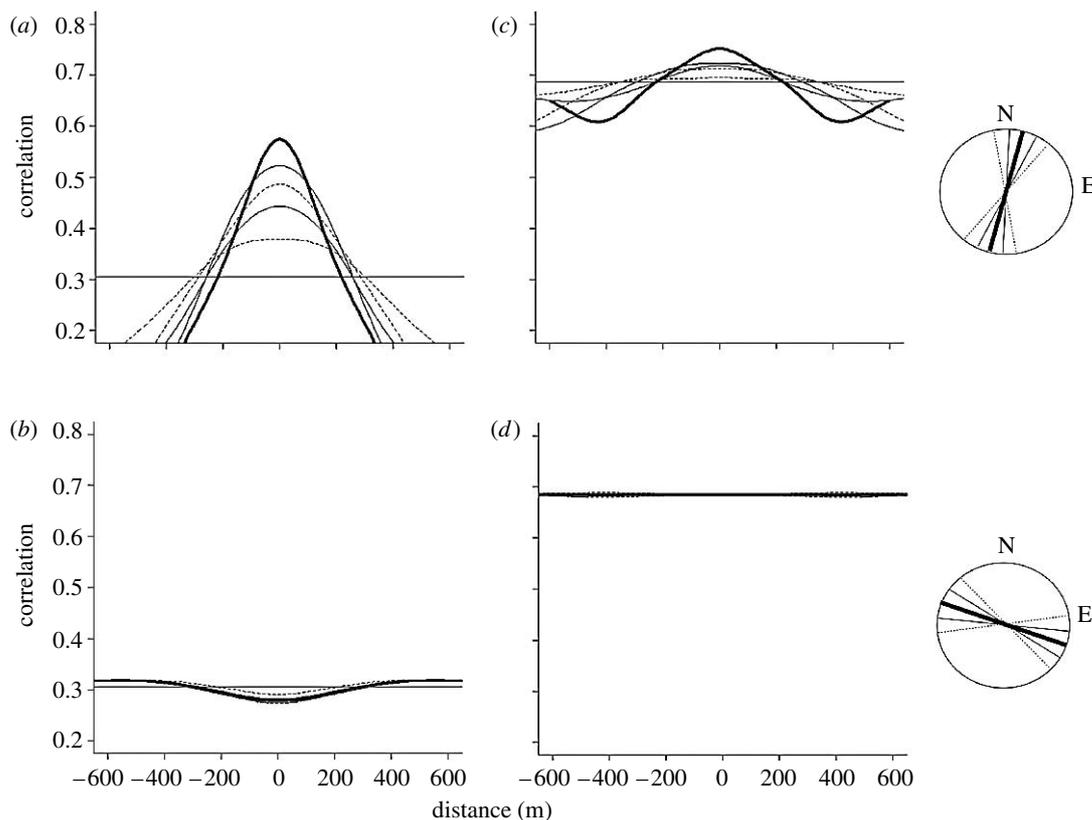


Figure 3. Directional spline correlograms for (a,b) *O. brumata* and (c,d) *E. autumnata* calculated for the mean orientation (thick solid line), $\pm 12^\circ$ and 24° (thin solid and dashed lines), in each of the two cardinal directions: (a,c) parallel to the altitudinal gradient and (b,d) perpendicular to the altitudinal gradient. The interval of $\pm 24^\circ$ roughly equals the observed circular variance around the mean orientation (49° and 55° parallel and perpendicular to the altitudinal gradient, respectively).

between the directional correlograms in this species (figure 3b,d). That is, the local *E. autumnata* populations peaked and declined quite simultaneously both at high and low altitudes (figure 4).

4. DISCUSSION

Altitudinal gradients are commonly used as a proxy for spatial climatic variation in ecology (Körner 2007). However, we are not aware of studies where altitude (or latitude) has been strategically used as a design measure to reveal impacts of climatic variation on spatial population synchrony. We propose that targeted population survey designs, with proper spatial replication of altitudinal transects, are suitable for revealing anisotropic synchrony patterns that may result from nonlinear population responses to climatic variation. As exemplified in figure 1, nonlinear demographic responses subject to spatial (i.e. altitudinal) and temporal (i.e. between-year) climatic variation will act to decouple the dynamics of populations located at different altitudes, whereas populations at the same altitude are expected to be more synchronized. Note that in the example in figure 1, the temporal variation in temperature may be perfectly correlated between altitudes, whereas population dynamics will not. As a matter of fact, nonlinear population responses to climatic variation violates the inherent assumption of linear environmental forcing in Moran's theorem, and then also the prediction arising that correlation in population dynamics should mirror the environmental correlation. Grenfell *et al.* (1998) emphasized how such a deviation from the Moran effect could indirectly originate from

complex interactions between nonlinear density dependence and climatic forcing. However, the most substantial forms of nonlinearity are likely to arise more simply from direct functional relations between demographic and climatic parameters (figure 1).

It should here be noted that anisotropy may also result from other deviations from Moran's theorem. For instance, spatially changing mechanisms of local population regulation violates the assumption of identical density-dependent structure across all populations considered. Hence strictly, nonlinear climate forcing is a sufficient, albeit not a necessary, condition for anisotropic synchrony patterns to emerge. Thus, as a rule pattern oriented approaches should, in the next research step, be followed up with mechanistic studies to identify the climate-sensitive demographic processes underlying spatio-temporal dynamics.

We expected that directional correlograms based on population time series from evenly spaced, replicated altitudinal transects would be able to discern the characteristic signature of anisotropy expected to result from nonlinear climatic forcing. In this case study, one of the species, namely *O. brumata*, exhibited the predicted anisotropic synchrony pattern. That is, the degree of synchrony dropped steeply across altitudes as to lose any clear signal of synchrony between populations at the treeline (240 m) and sea level (30 m), whereas there was no decrease in synchrony with distance within the same altitude. By contrast, *E. autumnata* did not exhibit any clear evidence for anisotropy as the degree of synchrony was globally high both between and within altitudes.

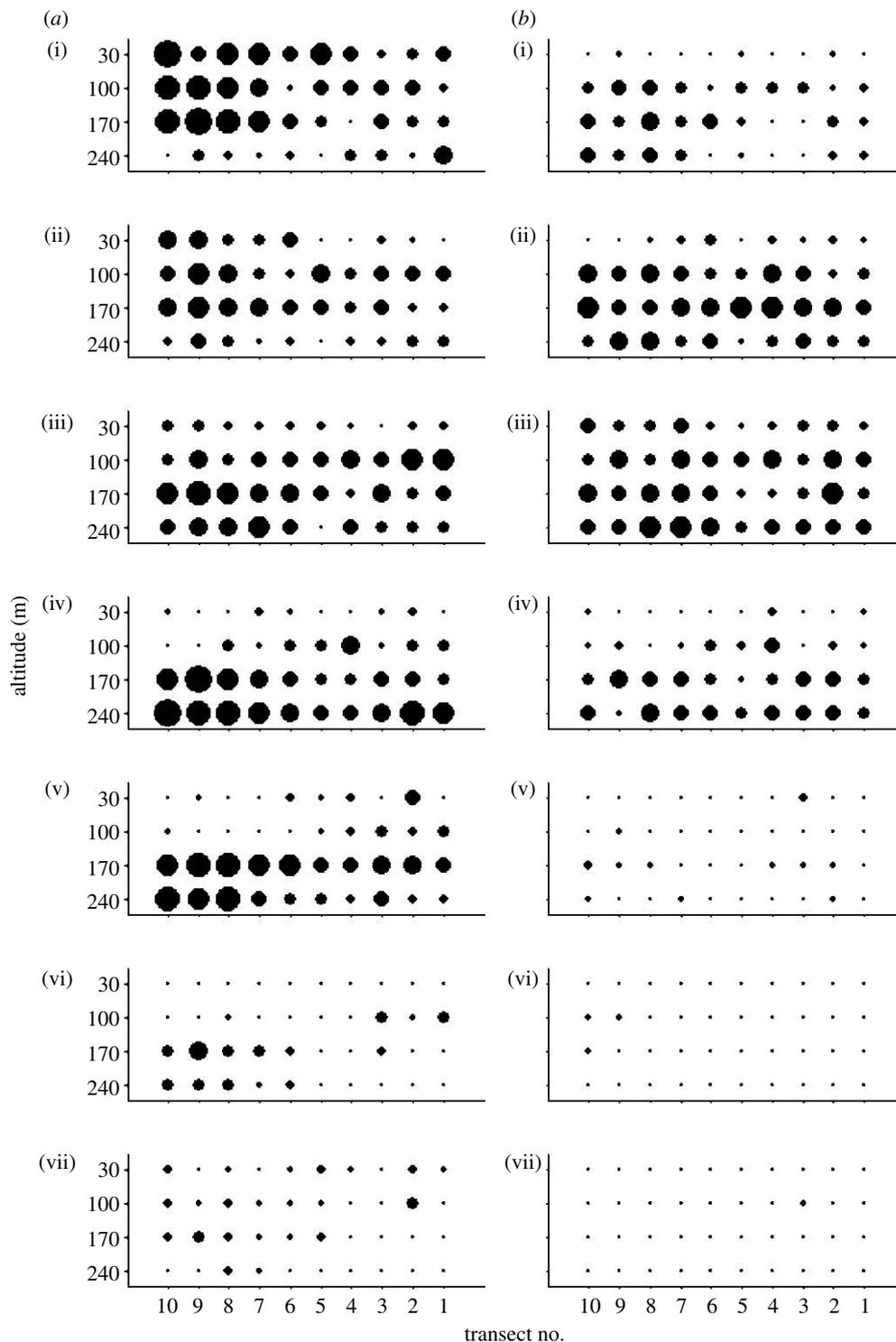


Figure 4. Relative population densities of (a) *O. brumata* and (b) *E. autumnata* along the 10 altitudinal transects in (i)–(vii) 2001–2007. The radii of the circles are proportional to log larval density.

The biology of the two geometrids is quite similar (Bylund 1999). The main host plant in Fennoscandia is the mountain birch (*Betula pubescens*). Both species have spring feeding larvae that need to appear synchronously with bud burst of their host plant. Moreover, the adults of both species emerge and breed in the autumn, and the eggs enter a winter diapause and hatch in spring. Still there are certain differences between the species in their response to seasonality and temperature that could account for the observed differences in their spatial population dynamics. For instance, the development rate of larvae of *O. brumata* is one instar delayed compared to

E. autumnata (Mjaaseth *et al.* 2005). Moreover, the period spent as pupae, which in both species is nonlinearly related to temperature (Peterson & Nilssen 1996, 1998), is considerably delayed in *O. brumata* compared to *E. autumnata* so that the former species ecloses as adult in the autumn three to four weeks later than the latter.

Although it is at this stage premature to speculate about which specific mechanism is likely to be most decisive, it is clear that such species differences in the timing of life stages can interact nonlinearly with spatial and temporal variation in climate as to cause the different spatial population dynamics. Specifically, we may infer from the

observed anisotropic synchrony pattern in *O. brumata* that this species is likely to have a high nonlinear sensitivity to climatic variation. Moreover, considering the mild winters in the study area, we can conclude that the climate sensitivity is due to other demographic parameters than egg survival, which previously has been most focused on in subarctic birch forest geometrids (Tenow 1996; Bylund 1999; Neuvonen *et al.* 1999). These inferences are in line with very recent observations of rapid, large-scale changes in the altitudinal (Hagen *et al.* 2007) and latitudinal (Jepsen *et al.* 2008) outbreak range of *O. brumata* in northern Fennoscandia, which has been attributed to the increasingly warmer springs (Jepsen *et al.* 2008). Indeed, it is the species exhibiting strongly anisotropic patterned population synchrony in climatic gradients, as indicated here for *O. brumata*, which might be expected to respond most abruptly to climate change.

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