

The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations

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Summary

1. Synchronous fluctuations of geographically separated populations are in general explained by the Moran effect, i.e. a common influence on the local population dynamics of environmental variables that are correlated in space. Empirical support for such a Moran effect has been difficult to provide, mainly due to problems separating out effects of local population dynamics, demographic stochasticity and dispersal that also influence the spatial scaling of population processes. Here we generalize the Moran effect by decomposing the spatial autocorrelation function for fluctuations in the size of great tit *Parus major* and blue tit *Cyanistes caeruleus* populations into components due to spatial correlations in the environmental noise, local differences in the strength of density regulation and the effects of demographic stochasticity.

2. Differences between localities in the strength of density dependence and nonlinearity in the density regulation had a small effect on population synchrony, whereas demographic stochasticity reduced the effects of the spatial correlation in environmental noise on the spatial correlations in population size by 21.7% and 23.3% in the great tit and blue tit, respectively.

3. Different environmental variables, such as beech mast and climate, induce a common environmental forcing on the dynamics of central European great and blue tit populations. This generates synchronous fluctuations in the size of populations located several hundred kilometres apart.

4. Although these environmental variables were autocorrelated over large areas, their contribution to the spatial synchrony in the population fluctuations differed, dependent on the spatial scaling of their effects on the local population dynamics. We also demonstrate that this effect can lead to the paradoxical result that a common environmental variable can induce spatial desynchronization of the population fluctuations.

5. This demonstrates that a proper understanding of the ecological consequences of environmental changes, especially those that occur simultaneously over large areas, will require information about the spatial scaling of their effects on local population dynamics.

Key-words: blue tit, density dependence, environmental stochasticity, great tit, Moran effect, population synchrony, spatial population dynamics.

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Introduction

Synchronous fluctuation in the size of populations that are widely separated in space is a striking biological phenomenon that has been documented in a wide range of taxa (Ranta, Kaitala & Lindström 1998; Bjørnstad, Ims & Lambin 1999; Koenig 1999; Liebhold, Koenig & Bjørnstad 2004). However, it has been difficult to quantify the contribution of different ecological mechanisms to the observed variation in the level of population synchrony (Bjørnstad *et al.* 1999). This in turn has reduced our ability to predict the population consequences of changes in the environment that occur simultaneously over large areas, such as expected changes in the climate (Houghton *et al.* 2001), which will affect population fluctuations both locally and regionally, and thereby the risk of extinction of populations (Engen, Lande & Sæther 2002a).

Spatial correlations in ecological variables caused by, for instance, similar climates, were initially suggested to be synchronizing agents for the fluctuations in size of spatially segregated populations. This led Moran, more than 50 years ago (1953), to develop one of the few quantitative predictions in population ecology. He predicted that if population synchrony is caused by correlation in an environmental variable, this should result in an autocorrelation in population fluctuations equal to the autocorrelation in environmental noise, assuming the same linear density regulation on a logarithmic scale in all populations. According to this Moran effect, the correlation in the fluctuations between two geographically separated populations will always be the same, irrespective of initial population sizes (Royama 1992).

Unfortunately, support for the idea of environmental variables as synchronizing agents in space for temporal variation in size or growth rates of populations has been difficult to find, except in only a few cases (Grenfell *et al.* 1998; Benton, Lapsley & Beckerman 2002). A pattern that often emerges is that when population synchrony is examined at large spatial scales; the spatial scaling of many environmental variables that are known to influence local population dynamics is often far larger than the scaling of the synchrony in the population fluctuations (Koenig 2001). Even in an experimental laboratory system in which different populations were provided food with a correlation of 1, the correlations in the popula-

tion fluctuations were still significantly smaller than 1 (Benton, Lapsley & Beckerman 2001). This may suggest that dispersal or the form of density regulation in the local dynamics (Ranta *et al.* 1998; Lande, Engen & Sæther 1999; Lundberg *et al.* 2000; Liebhold *et al.* 2004; Benton & Beckerman 2005; Ranta, Lundberg & Kaitala 2006), are more important in creating such synchronous fluctuations than any spatial covariation that exists in the environment.

The results of Moran (1953) are based on several simplifying assumptions (Ranta *et al.* 2006). First, a log-linear model of density regulation is assumed. Comparative studies of the population dynamics of birds have demonstrated that density dependence is not necessarily linear on a logarithmic scale (Sæther & Engen 2002; Sæther, Engen & Matthysen 2002a; Williams, Ives & Applegate 2003). Second, Moran (1953) assumed that environmental variables affect the local dynamics similarly over the entire geographical range (Lundberg *et al.* 2000). However, analyses of intraspecific variation in environmental influences on the population dynamics of several vertebrate species do indicate large regional variation in the impact of the same environmental variable on population fluctuations (Stenseth *et al.* 1999; Mysterud *et al.* 2000; Sæther *et al.* 2003). Theoretical analyses have shown (Engen & Sæther 2005) that relaxing those quite restrictive assumptions and generalizing the early results by Moran (1953) show that environmental variables may contribute substantially to population synchrony, although the spatial scaling of the synchrony may be far less than expected from the geographical scale of covariation in the environment.

Here we analyse patterns in the dynamics of great tit *Parus major* L. and blue tit *Cyanistes caeruleus* (L.) populations that have been studied for decades in several localities across central Europe. We will examine whether a common environmental forcing across larger distances on the population dynamics is present in those species by taking account of local variation in the population dynamics. We will then quantitatively analyse whether spatial heterogeneity in the contribution of different environmental variables to local population dynamics can explain any proportion of the spatial synchrony in the population fluctuations. In particular, we will examine the theoretical prediction (Engen & Sæther 2005) that an environmental variable that is

correlated over large areas can act to *desynchronize* the population dynamics if there are large differences among localities in its effect on the local dynamics.

Population model

Engen & Sæther (2005) derived a simple expression for the spatial synchrony in population fluctuations using the diffusion approximation to the theta-logistic model (Gilpin & Ayala 1973; Lande, Engen & Sæther 2003) with expected change in population size N from one year to the next equal to

$$E(\Delta N | N = n) = rn \left(1 - \frac{n^\theta - 1}{K^\theta - 1} \right). \quad \text{eqn 1}$$

The parameter r is the specific growth rate at population size $N = 1$, K is the carrying capacity and θ is a parameter in the theta-logistic model (Gilpin & Ayala 1973) determining the form of density regulation (Sæther *et al.* 2002a; Lande *et al.* 2003). Engen & Sæther (2005) derived a simple equation expressing the deviation from the Moran (1953)-effect due to nonlinearity in density regulation as well as in parameters describing the dynamics. The results were expressed in terms of a transformed population size,

$$g(N) = (1 - N^{-\theta})/\theta, \quad \text{eqn 2}$$

which turns out to have a rather simple linear type of dynamics. Following Engen & Sæther (2005) the spatial correlation between two transformed population sizes can be shown equal to

$$\rho_X = \rho_e \omega_d \omega_\theta \quad \text{eqn 3}$$

for small or moderate fluctuations around K . Here ρ_e is the spatial correlation between the environmental noise terms, and, using indices 1 and 2 for two populations at different locations, $\omega_d = 1/\sqrt{(1 + \varepsilon_1/K_1)(1 + \varepsilon_2/K_2)}$ represents the component due to demographic stochasticity and $\omega_\theta = \sqrt{(2\beta_1 - \theta_1^2\sigma_1^2)(2\beta_2 - \theta_2^2\sigma_2^2)/(\beta_1 + \beta_2 - \rho_e\sigma_1\sigma_2\theta_1\theta_2)}$ is the effect of spatial heterogeneity in the density regulation. Furthermore, σ_d^2 is the demographic variance, $\varepsilon = \sigma_d^2/\sigma_e^2$, $\sigma^2 = \sigma_e^2 + \sigma_d^2/K$ and the strength of density regulation at a scale of transformed population sizes $\beta = r/g(K) - (1/2)\theta\sigma^2$.

Our next step was to examine how the environmental stochasticity in the local dynamics can be partitioned into the effects of regional or local environmental covariates. Following Sæther *et al.* (2003; Sæther, Sutherland & Engen 2004b), we introduce environmental covariates as random effects in each locality by writing the effects of an environmental variable $Z = \tau V$ on the environmental noise term in the local population dynamics σ_e^2 as a linear function $\sigma_{res}^2 U + q\tau V$, where U and V are standard normal variates with zero means, τ is the standard deviation of Z , q is the regression coefficient expressing the effect

of Z and σ_{res}^2 is the variance in the local dynamics unexplained by Z . The proportion of the local dynamics explained by covariate Z becomes $p = q^2\tau^2/(\sigma_{res}^2 + q^2\tau^2)$. Finally, we express the environmental correlation ρ_e between localities 1 and 2 as a linear combination of the spatial covariation in the covariate Z , $\rho_Z = \text{corr}(Z_1, Z_2)$, and in the component unexplained by Z , $\rho_{res} = \text{corr}(U_1, U_2)$,

$$\rho_e = \rho_{res}\sqrt{(1-p_1)(1-p_2)} + \rho_Z \text{sign}(q_1, q_2)(\sqrt{p_1 p_2}), \quad \text{eqn 4}$$

where p denotes the proportion of variance of local dynamics explained by the covariate Z . Thus, the effect on the spatial environmental correlation ρ_e between localities 1 and 2 increases with the spatial correlation of Z if $\text{sign}(q_1, q_2) > 0$, but depends also upon how Z affects the local population dynamics.

A direct effect as well as a lagged effect of 1 year of the covariates was included in the analyses.

Methods and population model

STUDY POPULATIONS

This study is based on 28 great tit and 18 blue tit populations in central Europe that have been studied in 15 or more years (Fig. 1).

At all study sites the two species mainly breed in nest boxes. Thus, any bias in population estimates will be small.

ENVIRONMENTAL VARIABLES

The North Atlantic Oscillation (NAO) is a global climate phenomenon (Hurrell *et al.* 2003) expressed as an index based on the difference in normalized sea level pressures between Lisbon, Portugal and Stykkisholmur, Iceland, from 1864 through 2002 for the winter period

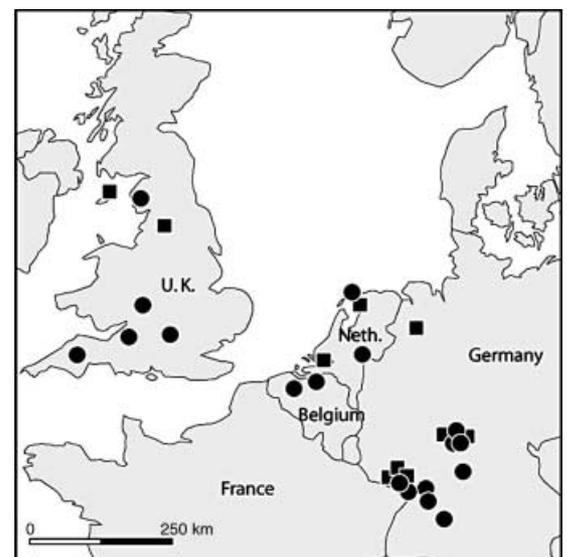


Fig. 1. The locations of population with time series of both great tit and blue tit (squares) or only the great tit (circles).

(see <http://www.cgd.ucar.edu/cas/climind>). A high positive NAO index is generally associated with relatively warm winters with a lot of precipitation in northern Atlantic coastal Europe, whereas low values of the index tend to result in cold winters with low levels of precipitation (Hurrell *et al.* 2003). NAO influences local population dynamics either through an effect on climate such as snow- or ice-cover or over larger areas (Engen *et al.* 2005; Grøtan *et al.* 2005) or influencing complex interactions among local climate variables (Hallett *et al.* 2004).

The production of superabundant seeds by different tree species, 'masting', has effects throughout many temperate ecosystems (Ostfeld & Keesing 2000; Koenig & Knops 2005) and has also been identified as an important factor in the population ecology of tits (Lebreton 1990; Slagsvold 1975; Perdeck, Visser & van Balen 2000). Data on annual variation in beech mast were collected at different localities in England (Packham & Hilton 2002), the Netherlands (Perdeck *et al.* 2000) and Germany (Zang 2003). Three levels of masting were used: (1) small; (2) moderate; and (3) high.

Data on monthly mean temperatures during the period January–July were obtained from local weather stations close to the study areas. We used monthly, bimonthly and 3-monthly means in the analyses.

ESTIMATING PARAMETERS

Estimates of the demographic variance σ_d^2 were obtained using individual based data for seven great tit and five blue tit populations. For those populations, in which no individual data were available, the mean values were used ($\bar{\sigma}_d^2 = 0.483$ and $\bar{\sigma}_d^2 = 0.415$ for great tits and blue tits, respectively). Because the contribution of σ_d^2 to the variance in the specific growth rate r (eqn 1) is density-dependent (Lande *et al.* 2003), we excluded populations in which $\hat{K} < 15$.

We modelled the density dependence using the discrete logistic model (May 1981). This model of density regulation is typical for many populations of passerine birds (Sæther *et al.* 2000, 2002b; Sæther & Engen 2002). We fitted the model following the approach by Sæther *et al.* (2002b) and Engen *et al.* (2005).

The spatial analysis of ρ_{res} is based on studying the residuals R_t obtained from fitting the model to time series observations at each location z ,

$$R_t(z) = \ln N_{t+1}(z) - E[\ln N_{t+1}(z) | \ln N_t(z), Y_t] \approx \sigma_e(z)U_e(z) + \sigma_d(z)U_d(z)/\sqrt{N_t(z)}, \quad \text{eqn 5}$$

where E is the estimated expected value using the discrete logistic model, Y_t denotes the vector of covariates and U_e and U_d are standard normal variates with zero means describing the environmental and demographic stochasticity, respectively.

We used the normal approximation and chose an exponential model for the spatial autocorrelation function ρ_e (Engen *et al.* 2005; Lillegård, Engen & Sæther 2005), characterized by the correlation at zero distance ρ_0 , the

correlation at very long distance ρ_∞ and the scaling l . Although several measures of the scaling of the spatial autocorrelation function have been suggested (e.g. Roughgarden 1977; Myers, Mertz & Bridson 1997), we here define scaling simply as the standard distribution of the autocorrelation function, following the approach by Lande *et al.* (1999). A graphical presentation of the parameters characterizing the autocorrelation function is found in fig. 1 in Lillegård *et al.* (2005).

The sampling properties of the estimates were found by parametric bootstrapping (Engen *et al.* 2005; Lillegård *et al.* 2005), simulating the residuals from the appropriate multinormal model as defined by the autocorrelation function, the distance matrix and estimates of local population parameters (Engen *et al.* 2005). We also computed the spatial correlation of the residual noise ρ_e obtained from fitting the dynamic model with covariate Z and a set of parameters (q_1, q_2) from two different sites. The significance of a change in the estimates was calculated by examining whether 0 was included in the appropriate lower and upper quantiles of the distribution of differences between the two bootstrap distributions (Lillegård *et al.* 2005).

Results

Because the spatial autocorrelation function for the transformed population sizes in ρ_X (eqn 3) is based on a continuous approximation, we first demonstrate its applicability in describing the dynamics of great tit and blue tit populations, which is modelled by the discrete logistic model. Assuming moderate fluctuations in population size, we assume that the total variance of the noise on the logarithmic scale is approximately a constant σ^2 and that expected dynamics at each locality is independent of its spatial location. For each pair of populations the parameter ρ_e is then calculated as the correlation between the environmental components of the noise terms. The factors ω_0 and ω_j in eqn 3 were found by inserting the estimates of the dynamical parameters of the two populations. These estimates of ρ_X can now be compared to the direct calculation of the correlations between the transformed population sizes ρ'_X . Figure 2 shows these two different estimates of ρ_X plotted against each other for each pair of populations.

Although the actual correlations in transformed population size were often slightly higher than those calculated from parameters characterizing the local population dynamical as well as the environmental covariation in space (Fig. 2), this still indicates that eqn 3 gives valid estimates of the correlation in temporal variation in size of two populations located at different localities. Furthermore, the spatial autocorrelation in population fluctuations decreased with distance between the localities in both great tit and blue tit (Fig. 3). In the great tit a significant ($P < 0.001$) common spatial component $\rho_{X,\infty}$ was present in the correlation at all localities, whereas in the blue tit the spatial autocorrelation approached zero at long distances.

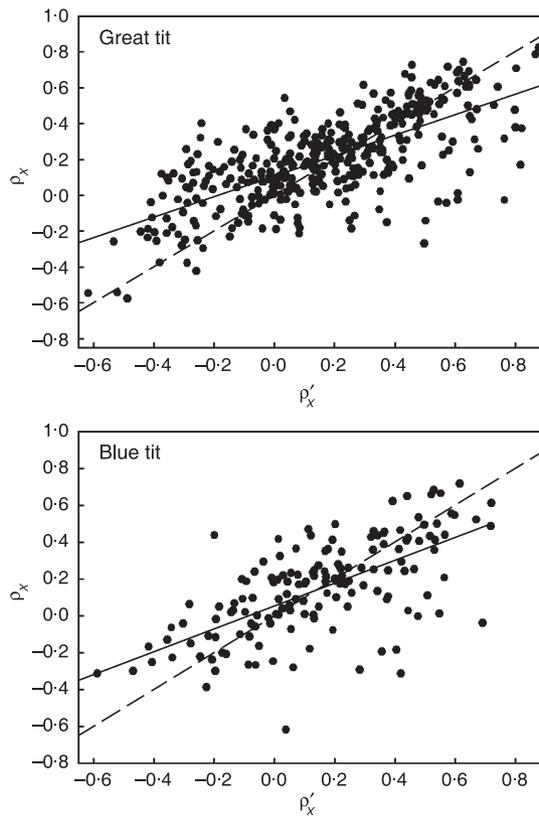


Fig. 2. The correlation in transformed population sizes (eqn 2) for each pair of populations calculated by using the estimates of local population parameters (eqn 3) ρ_x in relation to the actual correlation in transformed population size in the time series ρ'_x . The dashed line indicates the line with a slope of 1.

We can then use eqn 3 to decompose this spatial autocorrelation in population fluctuations into multiplicative components due to spatial heterogeneity in the effects of density regulation on local dynamics ω_0 , demographic stochasticity ω_d and the spatial correlation in the environmental noise ρ_e .

Local variation in the effects of density dependence on the population dynamics had a small effect on the population synchrony because the median value of factor ω_0 in eqn 3 was 0.929 and 0.928 for the great tit and the blue tit, respectively (Fig. 4).

In contrast, the effects of the component in the spatial autocorrelation due to demographic stochasticity on the population synchrony was larger (Fig. 5, the median value of ω_d was 0.793 and 0.767 for the great tit and blue tit, respectively). This shows that the spatial synchrony in the population dynamics was mainly generated by spatial correlation in the noise and was only to a small degree influenced by nonlinearity and local heterogeneity in the expected dynamics.

Although spatial covariation was found in the population fluctuations of both species (Fig. 3), the pattern of decay in synchrony with distance differed between the two species, which in turn was related to an interspecific difference in the pattern of spatial covariation in the environmental noise. In the great tit, a common

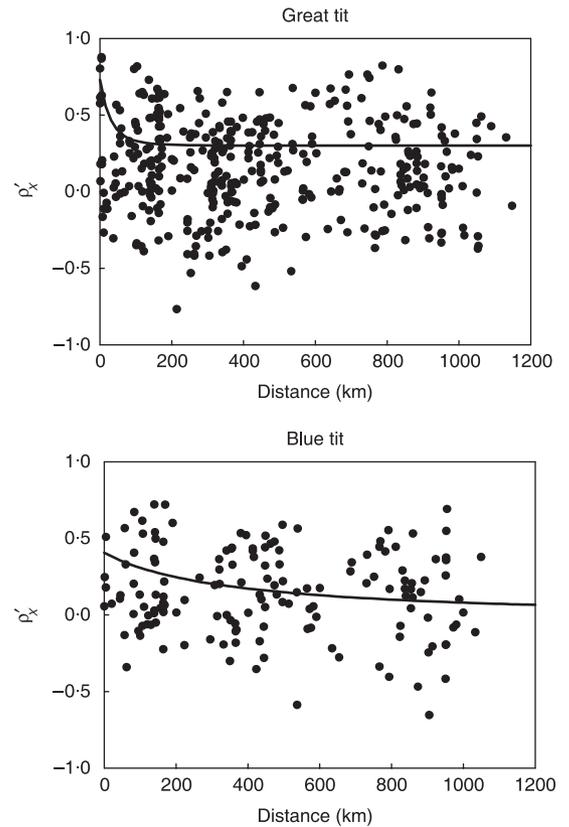


Fig. 3. The correlation ρ'_x between temporal variation in transformed sizes (eqn 2) of Great tit and Blue tit populations in Continental Europe as function of distance. The solid line denotes the 50% quantile of the bootstrap-distributions of ρ_x that were calculated (eqn 3) from the parameters describing ρ_e as well as those describing local dynamics. Because the local parameters r and K were approximately uncorrelated in space, a bootstrap-replicate of ρ_x was computed by first calculating a replicate of ρ_e , then choosing with replacement two sets of parameters (β , σ_e^2) from two different sites chosen at random and finally inserting these in eqn 3.

environmental force acted on all populations, giving an environmental correlation in the noise at infinite distances that was significantly ($P < 0.001$) greater than 0 (Fig. 6, $\hat{\rho}_{e,\infty} = 0.33$ (95% CI = 0.23–0.43)). In contrast, the blue tit data showed that no common environmental correlation was present at infinite distances (Fig. 6, $\hat{\rho}_{e,\infty} = 0$). This indicates a larger common environment component in the population dynamics of great tit than in the dynamics of the blue tit populations. However, there was a lower rate of decay with distance in environmentally induced covariation in population sizes in blue tits (spatial scaling of the environmental noise $\hat{l}_e = 380$ km (95% CI = 64–1665 km)) as compared with great tit populations ($\hat{l}_e = 34$ km (95% CI = 10–86 km); interspecific difference in l_e significant $P = 0.014$).

We then examined how different environmental variables affected the local dynamics of the two tit species. Variation in beech mast was found to strongly influence the population dynamics of most of the tit populations. In general, relatively large population sizes were found during breeding seasons following masting (Fig. 7,

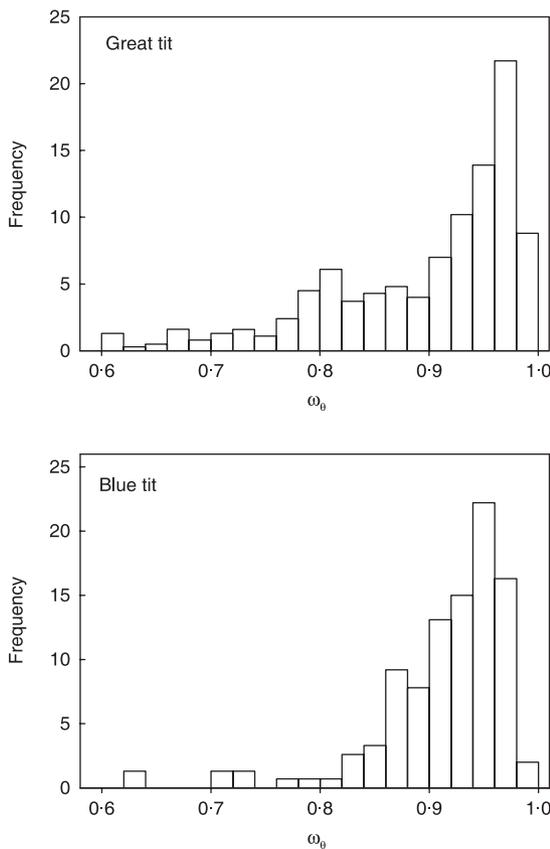


Fig. 4. The distribution for every pair of population of the factor $\omega_0 = \sqrt{(2\beta_1 - \sigma_1^2)(2\beta_2 - \sigma_2^2)}/(\beta_1 + \beta_2 - \rho_e \sigma_1 \sigma_2)$ (eqn 3) that for the logistic model ($\theta = 1$) gives the effects of spatial heterogeneity in local density regulation on the autocorrelation in the transformed population size ρ_x . Here β denotes for population 1 and 2 the strength of density regulation at the transformed population size, σ^2 the variance in the total noise and ρ_e the spatial autocorrelation in the environmental noise.

regression coefficient for the effects of the environmental covariate on the residual variation in the local dynamics $q > 0$ in 89.3% and 88.9% of great tit and blue tit populations, respectively).

This was normally followed by a population decrease in residual size (after correcting for density dependence) in the next year ($q < 0$ in 96.4% and 72.2% of great and blue tit populations, respectively). All together, beech mast in either year t or $t - 1$ explained a significant proportion of the residual variation in the size of 50% and 44% of great and blue tit populations, respectively. However, large differences were found among populations in the relative contribution of beech mast in year t (Fig. 7, $\bar{x} = 24 \pm 22$ (SD) % and $\bar{x} = 25 \pm 18$ (SD) % for the great tit and blue tit, respectively) or in year $t - 1$ ($\bar{x} = 18 \pm 22$ (SD) % and $\bar{x} = 16 \pm 25$ (SD) % for the great tit and blue tit, respectively) to the annual fluctuations in population sizes after accounting for the effects of density dependence and demographic stochasticity. In addition to beech mast, local climate and a regional climate variable, the NAO (Hurrell *et al.* 2003), affected the population dynamics of the two tit species. In both

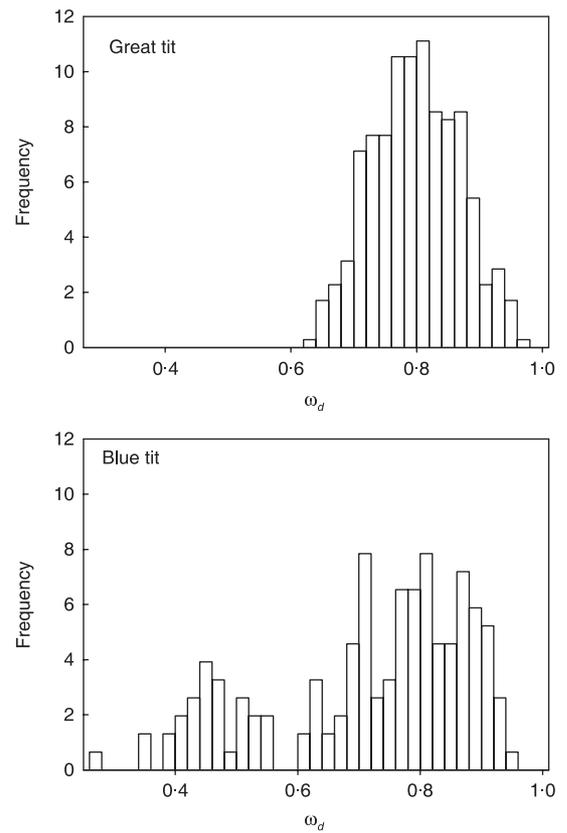


Fig. 5. The distribution for every pair of populations of the factor $\omega_d = 1/\sqrt{(1 + \varepsilon_1/K_1)(1 + \varepsilon_2/K_2)}$ (eqn 3) that denotes the effects of demographic stochasticity on the population synchrony ρ_x . Here K is the carrying capacity for population 1 and 2 and $\varepsilon = \sigma_d^2/\sigma_e^2$, in which σ_d^2 and σ_e^2 is the demographic and environmental variance, respectively.

species, temperature during February explained the highest mean proportion of the environmental variance ($\bar{x} = 14.3\%$ and $\bar{x} = 13.0\%$ for the great tit and blue tit, respectively). However, large regional variation in the direction of these climate effects was found in both species. In nine populations of each species, the regression coefficient q was positive ($P < 0.05$ in two of those), whereas a negative effect of February temperature was found in 19 great tit ($P < 0.05$ in five of those) and nine blue tit populations ($P = 0.005$ in one population). Similarly, large geographical variation was also found in the effects of NAO on tit population dynamics, with positive regression coefficients in 35.7% and 44.4% of the populations of great tits and blue tits, respectively.

These results demonstrate that density-independent environmental variables influence the dynamics of tit populations in central Europe. Next we examined the relative contribution of these variables to large-scale synchronous fluctuations of these tit populations. As is often the case for ecological variables (Koenig 1999, 2002), the two environmental covariates of importance for the local population dynamics of both species (Fig. 7) showed autocorrelations over large areas, with scaling $\hat{l} = 923$ km and $\hat{l} = 1299$ km for beech mast and

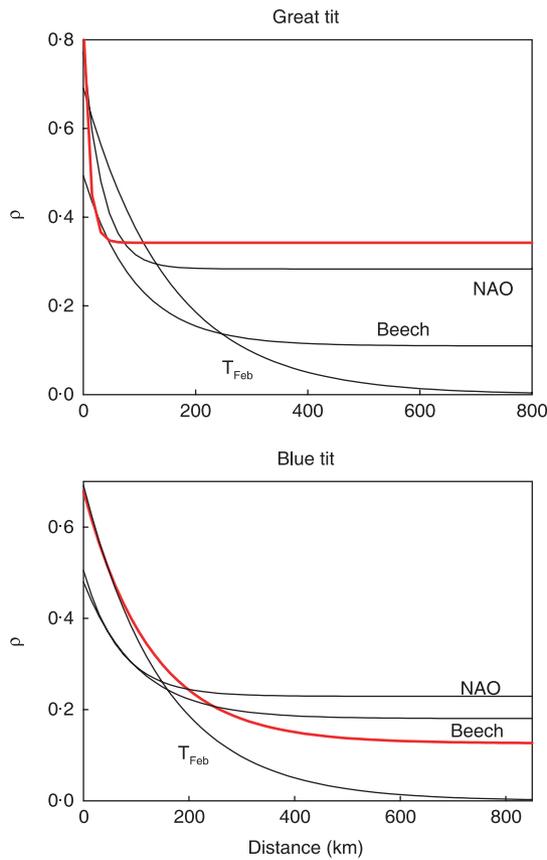


Fig. 6. The correlations in the fluctuations of great tit and blue tit populations in central Europe due to environmental covariation ρ_e as a function of distance (red line). Black lines denote the spatial autocorrelation in residuals that remain after accounting for the effects on local population dynamics of either beech mast, NAO or temperature during February.

February temperatures, respectively. However, there were differences in their contribution to the environmental component of spatial autocorrelation in the population dynamics. In the great tit, variation in beech mast explained a similar proportion of the spatial correlation at all distances (Fig. 6), but a significant ($P < 0.005$) proportion of the common noise still remained unexplained even at very long distances. A similar, but smaller effect of NAO was also found in this species. In contrast, in the blue tit, variation in beech mast as well as NAO explained a larger proportion of the synchrony at much shorter distances. At longer distances, these two variables acted so as to desynchronize the population fluctuations (Fig. 6), because the spatial correlation in the noise increased after accounting for their local effects. In both species, February temperature explained all of the common environmental noise at longer distances (Fig. 6). This shows that environmental variables that are highly correlated over larger areas may differ greatly in their influence on the spatial synchrony in population fluctuations, depending upon differences in spatial variation in local effects on population dynamics.

Discussion

Our analyses demonstrate that a common autocorrelation is present across central Europe in the fluctuations in the size of great tit and blue tit populations (Fig. 3). Spatial heterogeneity and nonlinearities in the dynamics reduced the spatial correlation in the population fluctuations ρ_x to 73.7% and 71.2% of the spatial correlation in the environmental noise ρ_e in the great tit and blue tit, respectively (Figs 4 and 5). Thus, the synchronous fluctuations in the size of spatially separated populations of these two species are to a large extent caused by the influence of environmental variables, such as the beech mast and temperature during February that are correlated in space over large areas (Fig. 6). This provides a quantitative demonstration, as predicted by Moran (1953), that environmental variables can synchronize population fluctuations over larger areas. However, the spatial scaling of population fluctuations is far less than the spatial scaling in the environmental variables because of regional variation in the strength of density dependence and environmental influences on the local population dynamics (Fig. 7). A similar pattern was also found in the effects of rainfall on the spatial synchrony in the dynamics of red kangaroos *Macropus rufus* Desmarest (Jonzén *et al.* 2005) as well as in a laboratory study of soil mites *Sansscassania berlesei* (Michael) (Benton *et al.* 2001).

Our approach allows the calculation of the effects of various factors, such as density dependence and demographic stochasticity, on the spatial autocorrelation (eqn 3). This enables us to quantitatively estimate the relative contribution of various factors to the population synchrony. Although this approach is based on several simplifying assumptions, the close relationship between the predicted correlation from eqn 3 and the actual correlation in transformed population sizes (Fig. 2) suggest that this may be a valid approach to model the spatial dynamics of tit populations. Another advantage is that many of the estimated parameters can be interpreted within a general theoretical framework that has been developed for analyses of spatial synchrony in population fluctuations (Lande *et al.* 1999; Engen *et al.* 2002a; Engen, Lande & Sæther 2002b).

In our study system nonlinearities and spatial heterogeneity in the local dynamics slightly reduced the effects of autocorrelation in the environmental noise on the synchrony in population fluctuations (Fig. 4). In a homogeneous environment, Engen & Sæther (2005) showed that the effects of variation in the form of density regulation on the spatial synchrony could be expressed as $\rho_x = \rho_e(1 - \delta)/(1 - \delta\rho_e)$, where $\delta \approx (\sigma^2/2r - \sigma^2)$ for the logistic model. In our study populations, we found that the mean of the estimates of these two parameters for all populations was $\bar{r} = 0.84$ and $\bar{\sigma}^2 = 0.0790$ for the great tit, and $\bar{r} = 0.80$ and $\bar{\sigma}^2 = 0.0794$ for the blue tit, giving $\hat{\delta} = 0.053$ and $\hat{\delta} = 0.10$ for the great tit and blue tit, respectively. Hence, nonlinearities in density dependence had only a small effect on the spatial synchrony in

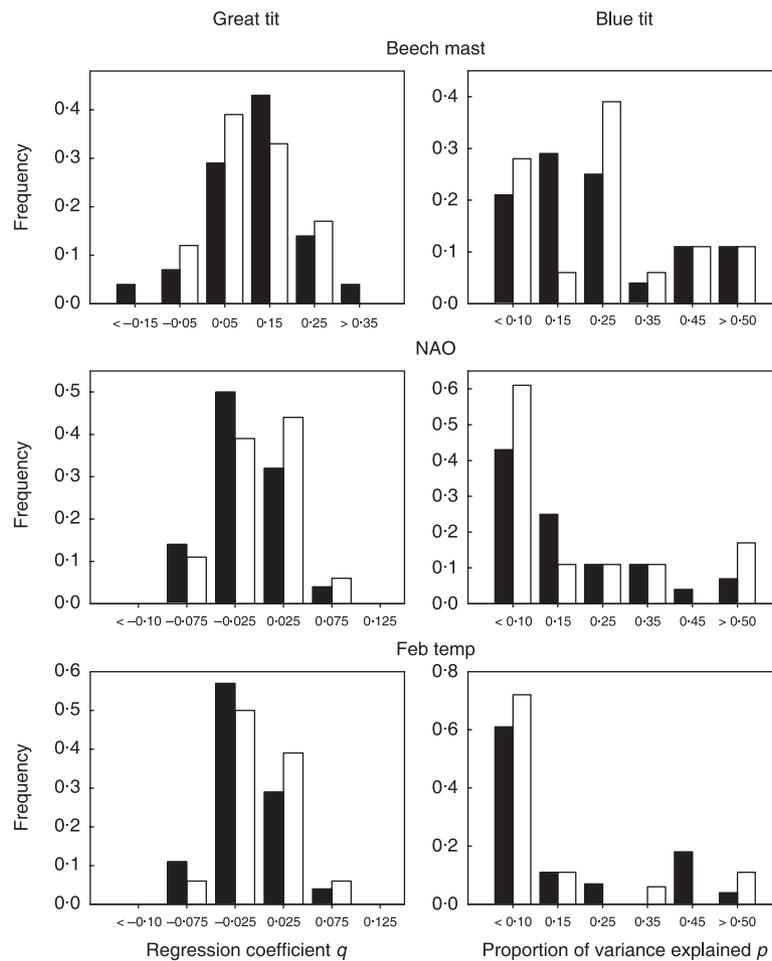


Fig. 7. The distribution of regression coefficients q and the proportion of the residual variation explained p for the effects of three environmental variables (beech mast, NAO and mean temperature during February) on the local dynamics of populations of great tits ($n = 28$) (black bars) and blue tits ($n = 28$) (white bars). Values represent residuals after controlling for density dependence and demographic stochasticity.

the fluctuations of the tit populations. Similarly, spatial heterogeneity in the strength of density regulation that also may affect the population synchrony (Engen & Sæther 2005) had a minor effect on ρ_x in both species.

In contrast, the influence of demographic stochasticity on the population synchrony was larger (Fig. 5). In general, demographic stochasticity acts to desynchronize the population fluctuations (Engen *et al.* 2005). In the present study, it reduced ρ_x by 21.7% and 23.3% relative to ρ_e in the great tit and blue tit, respectively (Fig. 5). Such an influence of demographic stochasticity on the spatial synchrony was due to a combined effect of the large demographic variance in both two species (Sæther *et al.* 2004a) and relatively small populations ($\bar{K} = 59 \pm 51$ and $\bar{K} = 50 \pm 73$ (SD) in the great tit and blue tit, respectively).

Variation in the size of the tit populations after accounting for the effects of density dependence and demographic stochasticity was influenced by environmental variables, such as beech mast and winter temperature during winter, especially during February (Fig. 7). This supports previous analyses of extrinsic influences on fluctuations in the size of tit populations (Slagsvold

1975; Bejer & Rudemo 1985; Dhondt *et al.* 1990; Lebreton 1990; Perdeck *et al.* 2000). As seems to be a general characteristic of the population dynamics of nonmigrant passerines at higher latitudes (Sæther *et al.* 2004b), fluctuations in population size is strongly affected by stochastic factors during the nonbreeding period. Our analyses showed that the beech mast, which for a long time has been known as a key environmental variable for tit population fluctuations (Perrins 1965, 1979; Lebreton 1990; Perdeck *et al.* 2000), on average explained only about 25% of the residual temporal variation in the population fluctuations after accounting for density dependence and demographic stochasticity. Similarly, in an analysis of climate influences on a large number of Norwegian roe deer *Capreolus capreolus* L. populations, snow depth during October to December explained a significant proportion of the annual variation in the change in size of 70.2% of the populations, with an average explained proportion of the residual variance of 21.3% (Grøtan *et al.* 2005). Furthermore, in the white stork *Ciconia ciconia* L. climate variables in general explained far less of the variance in the environmental stochasticity (Sæther *et al.* 2006). This suggests that

single climate variables rarely explains more than 20% of the residual variation in annual fluctuations in population size after accounting for the effects of density dependence and demographic stochasticity. One reason for this is covariation among different environmental variables that affect local population dynamics. For instance, as pointed out by Perrins (1965), the effects of the beech mast on tit populations may be stronger after mild than after cold winters.

An additional aspect of climate influences on tit population dynamics was that the direction of the effect of the same environmental variable could also differ among populations located close to each other (Fig. 7). For instance, changes in population size of both species were negatively associated with beech mast in the same two localities (in addition to one in which only great tit data were available). This shows that large spatial heterogeneity is often present in the effects of the same environmental variables on local population fluctuations (Stenseth *et al.* 1999; Myserud *et al.* 2000; Sæther *et al.* 2003, 2004b). Consequently, the presence of such spatial variation will according to eqn 4 reduce the impact on the spatial synchrony in the population fluctuations of an environmental covariate that in itself is correlated over large areas. Accordingly, in both species NAO had nearly a similar contribution the spatial synchrony in the population fluctuations, although it explained on average a smaller proportion of the local population fluctuations than the beech mast (Fig. 6). A similar spatial synchronizing effect of NAO have previously been found in the Continental great cormorant *Phalacrocorax carbo sinensis* L. (Engen *et al.* 2005).

Theoretical analyses have shown that in addition to environmental covariation in space, dispersal can influence the degree of synchrony in population fluctuations (Lande *et al.* 1999; Kendall *et al.* 2000). However, analysis of dispersal in the Belgian populations of great tits and blue tits (Tufto *et al.* 2005) indicated only short spatial scales of movement (dispersal standard deviations ranging from 0.7 km to 4.4 km). Such short movement distances are therefore unlikely to significantly affect the spatial scaling of noise in local population dynamics (Lande *et al.* 2003; Engen *et al.* 2005) because the density regulation in these populations is rather strong (the mean time to return to equilibrium $1/\bar{r} = 1.23$ years and 1.32 years for the great tit and blue tit, respectively).

This demonstration of an environmentally induced common component in the population dynamics of central European tit populations has three major implications. First, even with large spatial heterogeneity in local population dynamics and interchange of individuals between local populations, environmental variables can be the major synchronizing agents for the large-scale synchrony in population fluctuations. Second, theoretical studies have already shown that the presence of such autocorrelations in environmental variables, which have a common influence on populations separated in space, can affect important characteristics of populations, such

as the probability of extinction (Engen *et al.* 2002b) and the dynamical consequences of trophic interactions (Satake & Bjørnstad 2004). Third, our study shows that evaluating the ecological consequences of large-scale changes in the environment, such as expected climate change (Houghton *et al.* 2001), may be more difficult than previously realized because this requires that the spatial scaling of effects on local population dynamics are known. However, this study exemplifies that an extension of Moran's (1953) initial approach can improve our general insight into how such expected changes in climate will affect population dynamics at different geographical scales.

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