

# Spatial population dynamics: analyzing patterns and processes of population synchrony

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The large-scale spatial synchrony in the snowshoe hare (*Lepus americanus*) population density cycle, and its associated lynx (*Lynx canadensis*) cycle, stimulated P.A.P. Moran<sup>1</sup> to provide one of the first contributions to the discipline of spatial population dynamics. He developed statistical approaches for analysing spatial aspects of time series and formally derived a mechanism – later termed the Moran effect<sup>2,3</sup> – to explain the large-scale synchrony. Although the topic of spatial population synchrony, which we define as spatial covariation in population density fluctuations, was occasionally revisited in the decades following Moran's pioneering work<sup>4–6</sup>, it has recently become a major focus for investigation. New theoretical studies have suggested mechanisms for large-scale synchrony other than those suggested by Moran originally. A surge of pattern-oriented empirical studies have demonstrated not only that spatial population synchrony is a phenomenon that occurs widely in animals as well as plants, but also that the patterns of synchrony vary considerably<sup>7</sup>. These studies,

together with detailed theoretical studies, have shed new light onto key research issues in population ecology. For example, identifying the spatial extent of population synchrony points to which factors regulate populations and their 'characteristic' scale<sup>8,9</sup>. The spatial dimension has also provided alternative models for species coexistence and community structuring<sup>10,11</sup>. We are just beginning to understand how spatial and temporal population dynamics are integrated.

From an empirical point of view, it is of interest to obtain accurate estimates of the strength of synchrony as a function of isolation and spatial distance between populations. Central to the statistical analysis and estimation of synchrony from spatiotemporal data is the concept of spatial covariance (Box 1). The role of theory in this context is to predict what covariance patterns can arise from different ecological mechanisms and, eventually, how the resultant covariance patterns can feed back into (temporal) population dynamics<sup>12,13</sup>. The final, and perhaps most tricky, step in the interplay of theoretical and empirical approaches to spatial population dynamics is the empirical testing of the possible causal mechanisms.

**The search for mechanisms behind spatial population synchrony is currently a major issue in population ecology. Theoretical studies highlight how synchronizing mechanisms such as dispersal, regionally correlated climatic variables and mobile enemies might interact with local dynamics to produce different patterns of spatial covariance. Specialized statistical methods, applied to large-scale survey data, aid in testing the theoretical predictions with empirical estimates. Observational studies and experiments on the demography of local populations are paramount to identify the true ecological mechanisms. The recent achievements illustrate the power of combining theory, observation and/or experimentation and statistical modeling in the ecological research protocol.**

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The many recent achievements in theoretical spatial population dynamics have recently been subject to two thorough reviews and compilations<sup>10,11</sup>, while the empirical evidence for population synchrony has been reviewed by Koenig<sup>7</sup>. Here, we focus on the interplay between theoretical and empirical research protocols. We emphasize modeling results and statistical methodology that pertain to spatial covariance, because this is an important area where theoretical and empirical studies can meet. Research on population synchrony has now reached a stage where ecological theory and statistical methodology can guide the design of new empirical studies. Such studies will help to close the remaining gap between theory and data, and thus between observed patterns and underlying causal processes.

## Theory: predicting spatial covariance from ecological mechanisms

Theoretical models have been used to deduce patterns of population synchrony based on three classes of processes: (1) Diffusion or dispersal can induce varying levels of spatial synchrony by coupling locally regulated populations; the resultant synchrony can be fairly local in space or widespread<sup>13,14</sup>. (2) Community processes and trophic interactions can give rise to local or widespread synchrony in the prey or host populations because of the interactions between, and differential mobility of, the trophic interactants (e.g. predator–prey or parasite–host)<sup>9,15–17</sup>; models of such processes are often termed reaction–diffusion or activator–inhibitor models owing to the 'reaction' between the interactants and the activating or inhibiting effects they have on the local growth rates of each other. (3) The Moran effect describes how density-independent factors that are correlated across wide regions (e.g. climate or mast seed production) can synchronize the dynamics of populations; the central idea is that locally regulated populations will be synchronized if environmental shocks are globalized<sup>1–3,7</sup>.

The most complete body of theory predicting population synchrony from the three different synchronizing mechanisms is based on coupled map–lattice models<sup>11,18</sup> – that is, models of local populations that are coupled in a

**Box 1. Spatial covariance in population dynamics and related concepts**

**Spatial covariance** denotes the way the abundance or population growth rates covary in space (i.e. the way these properties depend statistically on neighboring, or more distant, populations). If the covariance is only a function of the distance between populations, it will not show any trends or directionality across space. Such covariance is **isotropic**.

**Anisotropic covariance** depends on direction as well as spatial distance.

**First order covariance** means that spatial processes such as dispersal operate at a local scale (e.g. only between neighboring populations). More distant covariance arises solely as a result of indirect effects. First order processes, with local positive correlations, have a covariance that declines monotonically towards zero with distance.

**The scale or extent of synchrony** is the distance at which the covariance is indistinguishable from zero (although other definitions can be used).

**Second (higher) order covariance** depends on more distant spatial units than the nearest neighborhood. Several ecological interactions, such as trophic interactions, can give rise to second order temporal covariance in dynamics – that is the population growth depends not only on the immediate past density, but also on prior generations. With localized movements such interactions can induce second order spatial covariance. Such covariance gives rise to spatially and temporally varying population synchrony that can be manifested as waves of abundance travelling through space.

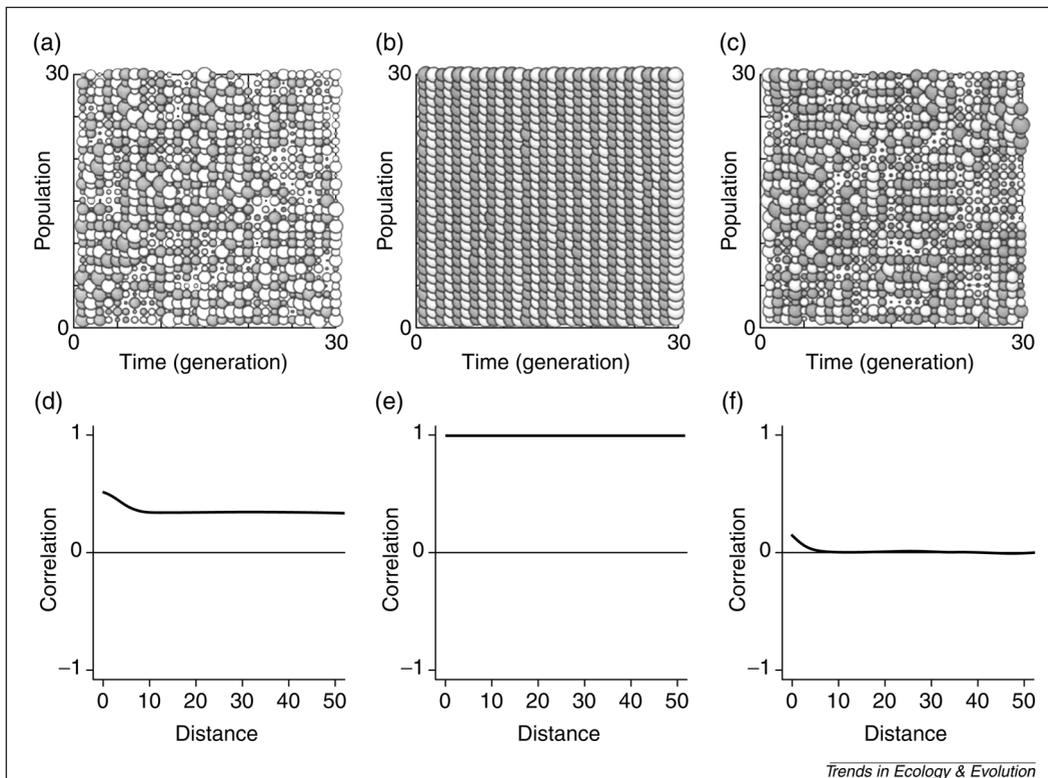
**Travelling waves** mean that peak densities are moving across space. The waves can be either unidirectional or of a radial or spiral type.

**Turing structures** are second order covariances that can also give rise to static, patchy patterns.

spatially explicit manner. In theory, each of the three mechanisms have the potential to induce large-scale (regional) population synchrony based on reasonable assumptions regarding dispersal rates and distances, and the frequencies and strength of environmental shocks. The crucial result is, therefore, that the different mechanisms leave characteristic signatures of spatial covariance that can be discerned in spatiotemporal data; that is, the spatial co-

This property of certain nonlinear systems is called phase-locking. By contrast, coupled populations with chaotic dynamics remain uncorrelated. Locally stable, and thereby approximately linear, populations follow Moran's theorem (which states that the correlation in dynamics should be equal to the correlation in the density-independent forcing agent<sup>2</sup>) (Fig. 1). The spatial dynamics of measles gives an empirical example of the subtle interaction between dynamic nonlinearities (which give rise to cyclic or chaotic dynamics) and synchrony: a change in disease transmission rates as a result of mass vaccination destroyed the high levels of synchrony between epidemics<sup>19</sup>. This is despite dispersal being, if anything, higher in the recent vaccination era.

Community processes lead to a variety of spatial patterns<sup>10,11,17</sup>, and thereby a variety of covariance patterns (Box 1). Nomadic avian predators can induce region-wide synchrony in their prey<sup>15</sup>. Both the degree of perfection of these predators' large-scale prey-tracking ability and their functional response at the local scale determine the strength of synchrony<sup>16</sup>. Furthermore, tight predator-prey interactions can result in cyclic dynamics, and either dispersal or correlated environmental shocks can subsequently induce regional phase-locking (Fig. 1b, Box 1). However, specialized host-enemy or predator-prey interactions can also give rise to second-order spatial covariance, which can take the form of travelling waves<sup>11,17</sup> or Turing structures<sup>11,20</sup> (Box 1).



**Fig. 1.** Ranta *et al.*<sup>13</sup> show how dispersal and environmental correlation result in different patterns of synchrony depending on the type of population dynamics in the evolution of 30 populations through time (30 generations) for the three types of dynamics: (a) stable local dynamics, (b) cyclic local dynamics and (c) chaotic local dynamics. Twenty-five percent of the local populations are allowed to disperse to neighboring populations in this simulation. The populations are affected further by correlated environmental stochasticity (spatial correlation = 0.3). White circles represent values smaller than the median, black circles represent values larger than the median. The areas are proportional to the absolute deviations from the median. (d–f) The corresponding spatial covariance as a function of distance. (d) The covariance of the locally stable populations is high between neighboring populations as a result of the dispersal, and decays to the level of the regional synchrony with distance (according to Moran's theorem). The average synchrony is 0.34. (e) Cyclic populations exhibit nonlinear phase-locking so that the populations are in synchrony throughout the region. The average synchrony is 0.98. (f) Chaotic populations exhibit little synchrony. The regionally correlated noise does not synchronize the dynamics; the average synchrony is 0.02 (Ref. 13).

Here, we emphasize two broad challenges that have great potential to narrow the current gap between theoretical and empirical studies of population synchrony. First, although different mechanisms sometimes lead to different predictions regarding the strength of synchrony (the most common predictions from models), any match between such predictions and estimates from spatiotemporal data cannot readily be used to exclude alternative mechanisms. For example, Moran effects are expected to cause large-scale synchrony. However, nonlinear phase-locking, caused by dispersal in cyclic populations, might be a viable alternative unless complementary information (e.g. regarding local dynamics) is available. By casting the predictions in specific functional forms of the covariance such ambiguities might potentially be removed. Second, different synchronizing mechanisms are likely to operate simultaneously in nature. The relative consequences of Moran effects and dispersal-induced synchrony have been investigated to some extent<sup>13</sup>. However, more theoretical work on how the different mechanisms interact to shape spatial covariance functions is needed. The extent to which the contributions of the different mechanisms are separable hinges on whether they operate in an additive fashion. Additivity, or lack thereof, is investigated most easily with strategic modeling.

**Statistics: quantifying spatial covariance**

The most common way to quantify the degree of synchrony between spatially segregated populations is to compute the ‘zero-lag cross-correlation’ between the time series of log-abundances<sup>7</sup> or growth rates<sup>21,22</sup> (Box 2). A common method to quantify region-wide synchrony is the average pairwise cross-correlation in the growth rates of populations (Box 2). Calculating region-wide synchrony is the natural first step in the study of population synchrony.

The next step in the analysis is to elucidate how synchrony drops with distance. Methodologically, there are two main approaches to this: the parametric and the non-parametric. When these synchrony-by-distance analyses suggest complex spatial covariance functions, specifically tailored analyses might be used to explore more fully the spatiotemporal dynamics. We will exemplify spatiotemporal dynamics with reference to travelling waves.

*Parametric covariance functions*

The parametric approach can be applied when a prediction about the functional relationship between synchrony and distance is formulated as a statistical model. Theoretical studies indicate that covariance functions take a variety of forms. As a possible yardstick model, a simple linear first-order spatial covariance process gives rise to a correlation that declines exponentially with distance. Myers *et al.*<sup>23</sup> thus conjectured that the spatial covariance in recruitment in a large number of fish species should exhibit an exponential decay.

The most commonly employed parametric approach has been to investigate the linear relationship between synchrony and distance in terms of the Pearson correlation coefficient<sup>3,24</sup> or the linear regression of synchrony on distance<sup>25</sup>. The *x*-intercept of this regression (the distance where the regression line is zero) has been used as a measure of the ‘extent’, or the scale, of synchrony. However, one of the main lessons from theoretical studies is that a linear decay in covariance with distance is not a likely outcome in nature. Therefore, other functional forms should be considered. Because the data exhibit interdependence, correct statistical inference for parametric covariance functions is obtained through randomization<sup>7</sup>.

**Box 2. Quantifying synchrony by means of cross-correlation**

The most commonly employed measure of synchrony between two populations, *i* and *j*, is the Pearson moment correlation between the two time series. By using **first-differenced** time series of log-abundance [i.e. using the difference between successive observations ( $\log N_t - \log N_{t-1} = z_t$ , where  $N_t$  is the abundance or density at time *t*)], emphasis is put on synchrony in population growth rates. Cross-correlation based on raw abundances can partly reflect long-term temporal trends in abundance; trends that potentially arise for different reasons in different populations. Some of the (positive or negative) correlation between time series of abundances might, therefore, be spurious. By contrast, cross-correlation based on growth rates focus on synchrony in change. Analyses can also be calculated on abundances corrected for local dynamics or trends by analysing the residuals from population models.

If the length of the time series is *T*+1, there will be *T* growth rates. We denote the mean growth rate of population *i* by:

$$\bar{z}_i \equiv \frac{1}{T} \sum_{t=1}^T z_{i,t}$$

and the variance by:

$$\delta_i^2 \equiv \frac{1}{T} \sum_{t=1}^T (z_{i,t} - \bar{z}_i)^2$$

The covariance in growths of populations *i* and *j* at lag zero is measured as:

$$\text{cov}(i,j) = \frac{1}{T} \sum_{t=1}^T (z_{i,t} - \bar{z}_i)(z_{j,t} - \bar{z}_j)$$

The corresponding **cross-correlation coefficient** is measured by:

$$\rho_{i,j} = \text{cov}(i,j) / \delta_i \delta_j$$

Because successive growth rates are strongly serially dependent, significance levels should be obtained by randomization<sup>7</sup>.

The mean or **region-wide synchrony** for *N* populations/time series is given by:

$$\text{average}(\rho_{ij}) = \frac{2}{N(N-1)} \sum_{i=1}^N \sum_{j=i+1}^N \rho_{ij}$$

The cross-correlation coefficients are not independent<sup>7</sup>. A bootstrap confidence interval for the mean synchrony is generated by sampling with replacement among the populations, with the subsequent recalculations of the coefficients and averages<sup>22</sup>.

When two independent synchronizing mechanisms are assumed to operate at different spatial scales, the signature of one mechanism is sometimes removed to highlight the effect of the other. For example, Paradis *et al.*<sup>33</sup> removed the common year-to-year trend, which they assumed to be caused by common climatic influences, to focus on the effect of species-specific dispersal ranges of British birds. Bolker and Grenfell<sup>19</sup> removed the correlation caused by seasonal cycles in measles dynamics (through a method called statistical prewhitening) to highlight the effect of vaccination on spatial synchrony.

The main strength of the parametric approach is that it can provide a strong link between theoretical and empirical analyses of population synchrony. When particular covariance functions follow from presumed synchronizing mechanisms, the parametric approach will facilitate rigorous statistical comparison of competing hypotheses. Furthermore, estimating parametric covariance functions permits quantitative synthesis and meta-analysis of independent studies. The main obstacle of the parametric approach is that current theory of population synchrony is not developed fully. Thus, the forms of the covariance functions that can arise from different synchronizing mechanisms are rarely known (but see Ref. 12).

*Nonparametric covariance functions*

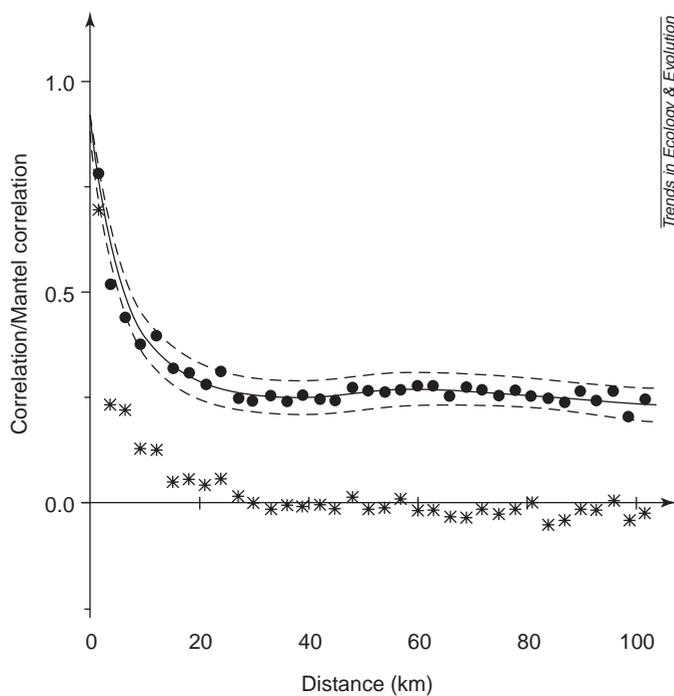
In response to the scarcity of theory pertaining to how the synchrony decays with distance, several researchers have tried to use nonparametric statistical approaches to estimate the functions. The Mantel correlogram approximates the relationship between synchrony and distance with

**Box 3. Estimating spatial covariance functions**

The distance,  $\delta_{ij}$ , between two populations,  $i$  and  $j$ , is usually measured by the geographic distance. However, sometimes the most appropriate distance is along river-systems or weighted according to how dispersal is impeded by different landscape features. The **Mantel correlogram**<sup>7</sup> decomposes the region-wide average synchrony (Box 2) by calculating a step function, obtained through local averaging around  $k$  focal spatial distances  $\{d_k; k = 1, \dots, K\}$ . These distances are usually selected at constant increments from the smallest to the largest distance observed. Before the calculation of averages, the  $\delta_{ij}$ 's (as defined in Box 2) are centered to have zero average by subtracting the overall mean,  $\rho$ . The Mantel correlogram,  $C(d_k)$ , is defined as:

$$C(d_k) = \text{mean}_k(\rho_{ij} - \bar{\rho} | L_k < \delta_{ij} \leq U_k) \quad (1)$$

where  $L_k$  and  $U_k$  signify the lower and upper tolerance limit around the  $k$  focal distances. The  $x$ -intercept of the Mantel correlogram measures the distance at which the synchrony is equal to the average synchrony, therefore, it is sometimes used as an estimate of the scale of local synchrony. Koenig's<sup>7</sup> **modified correlogram** does not center the  $\rho_{ij}$ 's. The modified correlogram thus has zero synchrony as the reference line<sup>26</sup> (Fig. 1).



(Online: Fig. 1)

Bjørnstad *et al.*<sup>22</sup> developed the **spline correlogram** as an adaptation of the **non-parametric covariance function**<sup>40</sup> (NCF). The spline correlogram provides a direct estimate of the covariance function itself. The nonparametric covariance function is calculated as:

$$\tilde{\rho}(\delta) = \frac{\sum_{i=1}^N \sum_{j=i+1}^N G(\delta_{ij}/h) \rho_{ij}}{\sum_{i=1}^N \sum_{j=i+1}^N G(\delta_{ij}/h)} \quad (2)$$

where  $G$  is a kernel function with kernel bandwidth  $h$  (see Ref. 41 for an introduction to kernel estimation). A confidence envelope can be calculated using the bootstrap<sup>22</sup>. Bjørnstad *et al.*<sup>22</sup> use the centered version of the spline correlogram (i.e. replacing  $\rho_{ij}$  in Eqn 1 with  $\rho_{ij} - \bar{\rho}$ ).

The figure depicts the spatial covariance in 30 years of census data of the Japanese wood mouse (*Apodemus speciosus*) from Northern Hokkaido, Japan<sup>22</sup>. The covariance is quantified by Mantel (asterisks) and modified (filled circles) correlograms, and by the (noncentered) nonparametric covariance function (unbroken line) applied to the growth rate of 179 populations spanning an area of  $150 \times 280$  km. The two latter methods show that the spatial correlation asymptotes to a region-wide synchrony around 0.2. The Mantel correlogram shows that the regional level of synchrony is reached at a distance of around 25 km. The 95% bootstrap confidence envelope of the nonparametric covariance function is shown by the dashed lines. Figure reproduced, with permission, from Ref. 22.

a discontinuous step function (Box 3). Because precision is lost when using a step function, a more novel approach, the nonparametric covariance function (NCF; Box 3) might prove more powerful. The NCF estimates a continuous function tailored specifically to represent a covariance function. The Mantel correlogram does not provide a confidence region for the spatial covariance, and therefore cannot fully address the presence of statistical difference in synchrony between different geographic regions or different species. By contrast, bootstrap confidence envelopes can be erected for the NCF. An analysis of two sympatric species of Japanese rodents (the grey-sided vole, *Clethrionomys rufocanus*; the Japanese wood mouse, *Apodemus speciosus*) using the NCF, demonstrated that the pattern of spatial synchrony differed significantly between the two species<sup>22</sup>.

The  $x$ -intercept of Mantel's correlogram represents the distance at which the synchrony is equal to the average synchrony for the entire sample of populations (Box 3). The correlogram has been used to distinguish between the extent of local synchrony (defined by the  $x$ -intercept) and region-wide average synchrony. For example, the extent of local synchrony among populations of bank voles (*Clethrionomys glareolus*) in southern Norway was inferred to be 30–40 km (Ref. 21). There are two snags to distinguishing local from regional synchrony. First, it assumes that the mechanisms causing local correlation are separable from those causing regional synchrony. Second, the region-wide average synchrony might depend on the extent of the study area. To circumvent this caveat of the Mantel correlogram, modified correlograms can be constructed that have zero synchrony as the reference line<sup>26</sup> (Box 3).

**Travelling waves**

Recent empirical studies have suggested second-order spatial covariance in spatially extensive survey data<sup>24,27</sup>. Elston and coworkers<sup>27,28</sup> have developed a statistical method to uncover the signature of travelling waves and estimate the waves' speed and direction (Box 4). Analyses of the data from a set of cyclic field vole (*Microtus agrestis*) populations in Scotland have revealed a wave in abundance that moved at an average speed of approximately 20 km per year in an east-northeasterly direction<sup>27</sup> (Box 4). Certain viral diseases, such as rabies, also exhibit pronounced travelling waves<sup>29</sup>. Such data sets are prime candidates for future study.

**Study design and complementary information**

Much of the data analyzed currently, stems from general surveys that were not designed to answer questions about population synchrony. More detailed considerations about spatial aspects of the sampling design, such as the size and shape of the study area (the sampling frame), and the spatial resolution and size of local sampling points (the grain), can improve studies of population synchrony. Sampling on too coarse a sampling grid could obscure local synchrony. When sampling small and very local populations, local sampling variance and demographic stochasticity might blur any existing covariance pattern further<sup>30</sup>. The sampling frame has bearings on several aspects of the estimated spatial covariance functions, because if it is too narrow compared with the scale of spatial variation, inference, with respect to spatial scaling, will be biased. For instance, the  $x$ -intercept of the Mantel correlogram, which measures the scale at which the synchrony is above the region-wide average (Box 3), will be a negatively biased estimate of the spatial correlation length if the size of the study area is too small. This effect is called the 'volume effect'<sup>31</sup>. A *post hoc* way to correct for design-based biases is to simulate data with known covariance

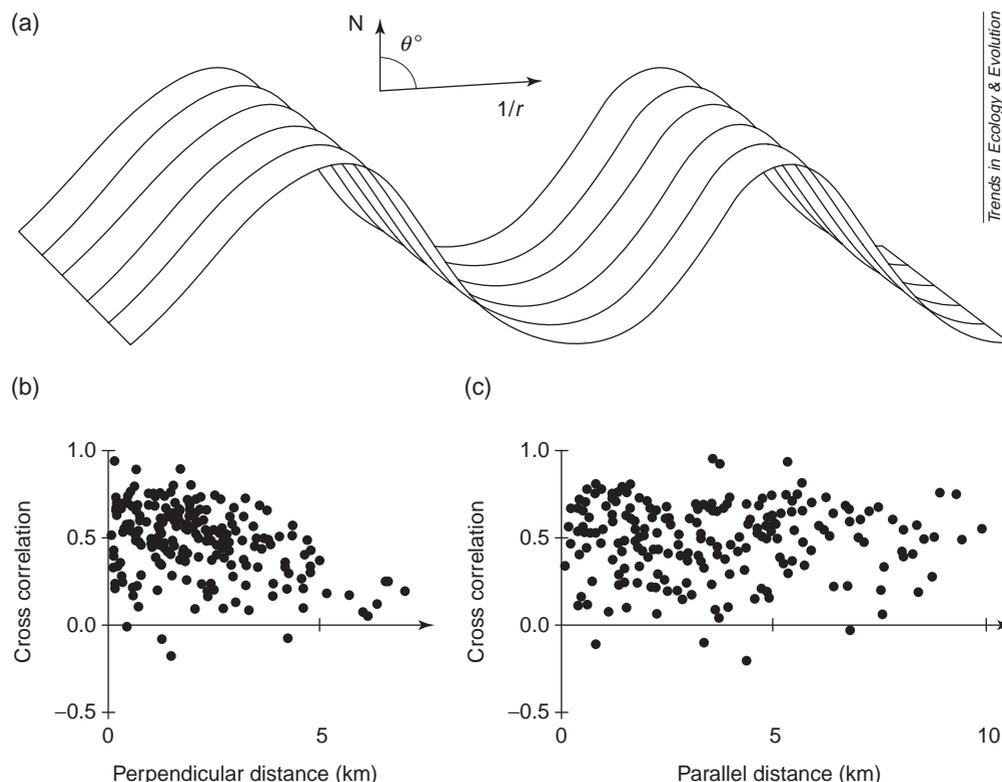
patterns on the map of the study area<sup>22</sup>. In addition, temporal aspects of the frame and grain should also be considered, because the pattern of synchrony might fluctuate on a long-term scale<sup>7,32</sup>. As for all ecological studies, the sampling design should be planned carefully and be guided by previous knowledge about the focal system, including preliminary observations of population dynamics and species-specific characteristics such as dispersal ranges.

Population ecologists are ultimately interested in the mechanisms behind any observed pattern. Unfortunately, there are limitations to what inferences can be made about mechanisms of population synchrony from survey data. *Post hoc* theoretical modeling<sup>24</sup> might serve to narrow the set of mechanisms to some trophic mechanism, but there are still several candidates. Complementary approaches are needed to understand population synchrony.

Comparative analyses of patterns of synchrony in species with different mobility have provided the main source of insight to the role of dispersal so far. In multi-species data sets of a diversity of insects<sup>25</sup> and birds<sup>33</sup>, local synchrony was most extensive in the most vagile species. However, the opposite was observed for two sympatric rodents<sup>22</sup>. Observational studies, eliminating certain synchronizing agents by design, are valuable; the Moran effect was concluded to be the likely mechanism synchronizing two island populations of Soay sheep (*Ovis aries*)<sup>34</sup>. In the more common situations where there are no, or incomplete, barriers to dispersal, the extent of the dispersal should be measured. Stacy *et al.*<sup>35</sup> used genetic markers and the lack of gene flow to dismiss dispersal as the synchronizing mechanism in boreal bank voles. In cases where dispersal is prevalent on a scale that can cause synchrony, inference is difficult. First, transfer rates between populations are inherently difficult to estimate<sup>36</sup>. Second, these estimated rates are usually subsequently implemented in models in the form of diffusion coefficients. Because such coefficients are scaled to time, care must be exerted in choosing appropriate time-scales. Third, simple models assume constant dispersal rates, whereas in reality these can vary with density and other ecological circumstances. For instance, lynx and coyotes (*Canis latrans*) adopt

### Box 4. Quantifying travelling waves

Elston and co-workers<sup>27,28</sup> developed a modeling approach to estimate the speed, direction and statistical significance of travelling waves. (a) The wave can take different shapes but is assumed to travel as a parallel, unidirectional wavefront with a bearing  $\theta$  and a time invariant speed  $1/r$ . At any given time the abundance of populations located perpendicular to the wave front becomes progressively dissimilar with distance. This induces anisotropy in the spatial covariance. (b) The anisotropy is seen clearly in the data on cyclic field vole populations in Scotland<sup>27</sup>. The drop in cross-correlation is conspicuous in the direction perpendicular to the wavefront (72°N). (c) The correlation does not decline with distance parallel to the wave front (along a bearing of 162°N). *Reproduced, with permission, from Ref. 27.*



(Online: Fig. 1)

In the model used to estimate speed and bearing of the wave (Eqn 1), the dynamics of all populations are assumed to follow the same pattern of temporal fluctuations,  $S$ , but the timing depends on the population's spatial location (the  $x$ - and  $y$ -coordinate) along the direction of the wave. We denote this distance by  $D(x_i, y_i, \theta)$ . The local abundance  $N_{i,t}$  of population  $i$  at time  $t$  is thus modeled according to:

$$\log N_{i,t} = u + S[t + rD(x_i, y_i, \theta)] + e_{i,t} \quad (1)$$

where  $u$  is the grand mean abundance and  $e_{i,t}$  are the residuals. To allow flexibility in the shape of the population fluctuations (and thereby also the shape of the travelling wave),  $S$  is fitted as a smoothing spline in a generalized additive model<sup>41</sup>. The estimation of  $r$  and  $\theta$  is calculated using profile likelihood<sup>28</sup>. (Hilborn and Mangel<sup>42</sup> provide an introduction to profile likelihood methods.) As the error term  $e_{i,t}$  is likely to be spatiotemporally correlated under this model, statistical significance is assessed through randomization tests<sup>28</sup>.

The wave speed is believed to change both in cyclic field vole data<sup>27</sup>, and in cyclic snow shoe hare data<sup>37</sup>. Recent extensions of the model allow for varying the speed,  $1/r$ , across time or cycle phase<sup>28</sup>.

a nomadic lifestyle following crashes in snowshoe hares<sup>37</sup>. These changes in predator spatial behavior are likely to influence synchrony and dynamics in both prey and predator<sup>37</sup>.

The mechanisms behind large- and local-scale synchrony are interpreted most easily through studies of local demographic rates. Estimates of emigration and immigration rates of populations, as well as measures of mortality caused by putative synchronizing agents, will highlight their relative influences. Because of the large spatial scale of population synchrony in many species, it is often thought that experimental studies would be impossible to conduct. However, experimentation is a powerful tool for highlighting determinants of local demography. Exclosures and/or enclosures, large enough to include local populations, can be used strategically as complete or partial barriers against migration and the influx of trophic interactants. Such exclosure studies

have been used to examine effects on local demography in small mammals, but have yet to be coupled to large-scale dynamics. In some cases, the entire focal system is sufficiently small-scaled that manipulations are possible<sup>38</sup>. Recent studies by Harrison and co-workers<sup>20,39</sup> show how diffusive interactions in insect parasitoid–host systems cause spatiotemporal patterns in abundance and mortality as predicted by spatial predator–prey theory. These studies combine experimentation, statistical analysis and theoretical modeling to understand spatial dynamics.

### Conclusion and prospects

We have highlighted various aspects of the interplay between theory and empirical studies for understanding the patterns and mechanism of spatial population synchrony and covariance. The spatial covariance function provides one natural intersection between models and data, statistical models for spatial variation in abundance provide another, but only if tightly motivated by ecological theory. Recent statistical developments provide the means for more studies that link theory and data. To identify the underlying mechanisms of population synchrony, specifically tailored study designs are useful. Preferably, these should include experiments on local populations, because determinants of large-scale population synchrony ultimately exert their influence via local demographic rates (mortality, reproduction and recruitment). Different patterns of local fluctuations in abundance change the synchronizing effect of dispersal and regional disturbances. This effect illustrates how local and large-scaled factors are intimately linked in shaping population synchrony.

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