

# SPATIAL SYNCHRONY IN POPULATION DYNAMICS\*

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■ **Abstract** Spatial synchrony refers to coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations. This phenomenon has been documented in the dynamics of species representing a variety of taxa and ecological roles. Synchrony may arise from three primary mechanisms: (a) dispersal among populations, reducing the size of relatively large populations and increasing relatively small ones; (b) congruent dependence of population dynamics on a synchronous exogenous random factor such as temperature or rainfall, a phenomenon known as the “Moran effect”; and (c) trophic interactions with populations of other species that are themselves spatially synchronous or mobile. Identification of the causes of synchrony is often difficult. In addition to intraspecific synchrony, there are many examples of synchrony among populations of different species, the causes of which are similarly complex and difficult to identify. Furthermore, some populations may exhibit complex spatial dynamics such as spiral waves and chaos. Statistical tests based on phase coherence and/or time-lagged spatial correlation are required to characterize these more complex patterns of spatial dynamics fully.

## INTRODUCTION

The quest to understand mechanisms behind the spatiotemporal dynamics of natural populations has been a force motivating studies of animal and plant populations for more than a century. Intensive studies on individual species have yielded information useful for describing the important roles that trophic interactions and exogenous forces play in specific systems. However, for most species we still lack a predictive understanding of the causes of population fluctuations.

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Because of the difficulty in determining the importance of specific ecological processes, many recent studies have attempted to infer mechanisms indirectly via the analysis of population time series (Kendall et al. 1999, Royama 1981, Turchin 1990). These studies characterize temporal patterns (measured by autocorrelation functions, periodograms and similar types of analytical techniques) and use this information to infer the relative role of biotic and abiotic forces in temporal dynamics. The recent flurry of studies on population synchrony may be seen as advancing this line of inquiry to include spatiotemporal dynamics. Population synchrony, as measured by correlation in abundance (or changes in abundance), was extensively studied starting in the 1990s (reviewed in Bjørnstad et al. 1999a, Koenig 1999). These types of studies have continued to advance in scope, and recently there have been important innovations to the analysis of spatial dynamics via the application of phase analyses. These methods have expanded our characterization of spatial dynamics beyond detection of simple synchrony to include more complex patterns of spatial dynamics such as waves.

A perpetual limitation in the analysis of dynamics of multiple populations has been the overwhelming complexity of analyzing large quantities of spatially referenced time series data. However, with the advent of geographical information systems, faster and cheaper computers, more powerful spatial statistics, and greater access to data, dealing with such large and complex datasets is no longer the insurmountable problem it was a few decades ago. Results from many such analyses indicate that different populations of the same species often fluctuate more or less synchronously, even when populations are quite distant from each other. Specifically, increases and decreases in abundance of one population tend to occur simultaneously with increases and decreases of other populations. As the distance separating populations increases, synchrony typically declines. This phenomenon may reflect two different patterns: for populations that fluctuate in a nonperiodic fashion, the pattern of fluctuation may become increasingly dissimilar with distance. For populations that fluctuate in a cyclic or quasiperiodic fashion, the populations' cycle phase may diverge with separation distance.

The world around us is a spatially autocorrelated place (Legendre 1993). In any biotic or abiotic property, such as elevation, temperature, population density, or reproductive rate, values at nearby locations tend to be similar (Rossi et al. 1992). However, spatial synchrony is a special type of spatial autocorrelation in that synchrony refers to spatial autocorrelation of variation through time. This special type of space-time variation sets it apart from other spatially autocorrelated properties.

Simultaneous with the advent of analytical studies of space-time patterns in real populations has been a blossoming of theoretical studies of spatial dynamics, both with respect to spatially extended populations (e.g., Bascompte & Sole 1998a) and metapopulations (e.g., Hanski 1998). Population models have been useful instruments for testing hypotheses concerning the mechanisms behind spatial synchrony. In any model in which two or more populations are allowed to fluctuate according to some mixture of density-dependent and density-independent

processes, three mechanisms may cause synchrony: (a) dispersal among populations; (b) synchronous stochastic effects, often referred to as the “Moran effect”; and (c) trophic interactions with other species that are themselves either synchronized or mobile. As in many other ecological problems, linking theory to reality is often challenging. Although it is possible to identify these synchronizing processes in models, identification of the dominant synchronizing processes in field populations is often more difficult because all three mechanisms may produce nearly identical signatures of synchrony among populations. Ecologists are often frustrated in their efforts to identify the cause of synchrony, but this quest poses an exciting challenge to population ecologists, and many methods have been described for drawing mechanistic inferences.

## THE UBIQUITOUS PRESENCE OF SPATIAL SYNCHRONY IN POPULATION DYNAMICS

Spatial synchrony of abundance has been found in populations representing virtually all major taxa and ecological roles (Table 1). Given that any two subunits of the same population are, in theory, perfectly synchronized if there is no distance separating them (in which case in a practical sense they should be considered the same population), spatial synchrony is, not surprisingly, common among nearby populations. However, researchers have observed considerable variation in the geographical range of synchrony in studies of various organisms, only some of which can be attributed to differences in scale intrinsic to the organism itself. The observed range of spatial synchrony is a few centimeters in microcosm experiments with protozoa to hundreds or thousands of kilometers in numerous “free-ranging” systems (Table 1). Synchrony usually decreases as the distance between populations increases (Ranta et al. 1995a, Sutcliffe et al. 1996, Bjørnstad et al. 1999a); however, traveling population waves can lead to U-shaped (Ranta & Kaitala 1997) or cyclic (Bjørnstad & Bascompte 2001) relationships between synchrony and distance.

In addition to synchrony of abundance, specific demographic properties, such as reproduction or mortality, and even population characteristics, such as mean size and age distributions, may be spatially correlated. In particular, many plant species exhibit a phenomenon, known as “masting” or “mast seeding,” in which temporal variation in reproduction is highly synchronized among individual plants (Koenig et al. 1999, Kelly & Sork 2002, Liebhold et al. 2004). Comparable patterns of spatially synchronous reproductive dynamics have been observed in animals as well (Ims 1990, Myers et al. 1995). More recently, other kinds of demographic factors, such as the sex ratio of goshawk (*Accipiter gentiles*) nestlings (Byholm et al. 2002) and age- and size-distributions of California tiger salamanders (*Ambystoma californiense*) in ponds (Trenham et al. 2001) have been found to exhibit significant spatial synchrony. Mortality may also be synchronized among spatially disjunct populations as a consequence of spatially synchronous disease dynamics (Viboud et al. 2004).

**TABLE 1** Summary of records of intraspecific spatially synchronous population dynamics among all taxa

<b>Taxa</b>	<b>Geographical extent of synchrony</b>	<b>References</b>
Protista: ciliophora	10–500 cm (microcosm)	Holyoak & Lawler 1996
Fungal plant pathogen	0.5–3 km	Thrall et al. 2001
Viral human pathogen	1–1000 km	Bolker & Grenfell 1996, Rohani et al. 1999, Viboud et al. 2004
Insect detritivores	5–20 m	Tobin & Bjørnstad 2003
Insect herbivores	1–1000 km	Hanski & Woiwod 1993; Hawkins & Holyoak 1998; Liebhold et al. 1996; Liebhold & Kamata 2000; Myers 1990, 1998; Peltonen & Hanski 1991; Peltonen et al. 2002; Pollard 1991; Raimondo et al. 2004; Rossi & Fowler 2003; Shepherd et al. 1988; Sutcliffe et al. 1996; Tenow 1972; Williams & Liebhold 1995, 2000b; Zhang & Alfaro 2003
Insect predators and parasitoids	10 m–400 km	Baars & Van Dijk 1984, Rossi & Fowler 2003, Satake et al. 2004, Tobin & Bjørnstad 2003
Fish	10–500 km	Fromentin et al. 2000; Myers et al. 1995, 1997; Ranta et al. 1995a
Amphibians	0.2–100 km	Trenham et al. 2001, 2003
Birds	5–2000 km	Bellamy et al. 2003; Bock & Lepthien 1976; Cattadori et al. 1999; Jones et al. 2003; Small et al. 1993; Ranta et al. 1995a,b; Koenig 1998, 2001, 2002; Moss et al. 2000; Paradis et al. 1999, 2000; Watson et al. 2000
Mammals	10–1000 km	Bjørnstad et al. 1999b; Christiansen 1983; Elton & Nicholson 1942; Grenfell et al. 1998; Ims & Andreassen 2000; Mackin-Rogalska & Nabaglo 1990; Moran 1953b; Post & Forchhammer 2002; Ranta et al. 1995a,b, 1997a,b, 1998; Small et al. 1993; Smith 1983; Swanson & Johnson 1999
Mollusks	2–30 km	Burrows et al. 2002

These examples of population synchrony all involve geographically disjunct populations of the same species. However, there have been numerous observations of synchronous fluctuations among different species as well. Many examples of interspecific synchrony can be found between pairs of species that have direct trophic interactions, such as predators and their prey. Numerical responses seen in trophic interactions often lag each other in time, which can result in time-lagged synchrony. Note, for instance, that the classic Lotka-Volterra models produce cycles in which the predator peak lags that of the prey by one-quarter-cycle length. Alternative prey species that share a common predator, a situation referred to as “apparent competition,” may as a result be forced into synchrony (Bulmer 1975, Small et al. 1993, de Roos et al. 1998, Jones et al. 2003). Similar synchronization may occur among species that share a fluctuating food resource (Bock & Lepthien 1976, Koenig 2001, Jones et al. 2003). Numerical tracking of prey populations by predator populations can lead to synchrony, as illustrated by interspecific synchrony between mast-seeding plants and their seed predators (Curran & Webb 2000, Schaubert et al. 2002, Satake et al. 2004). Synchrony has also been observed among populations of sympatric species that are not directly linked through trophic interactions, such as herbivorous forest insects (Miller & Epstein 1986, Hawkins & Holyoak 1998, Myers 1998, Raimondo et al. 2004) and allopatric large herbivores (Post & Forchhammer 2002).

## MEASURING SYNCHRONY

Early studies relied on visual inspection of data to assess synchrony (e.g., Elton 1942). The current tradition, however, is to rely on formal statistical analyses. This, in turn, requires strict numerical definition of synchrony. Several alternative and/or complementary definitions exist. Crudely speaking, these methods may be divided into those measuring synchrony and those measuring phase synchrony (sometimes called phase coherence). An obvious measure of synchrony is the correlation between two time series of abundance. Correlation is here usually measured (albeit not necessarily) by the Pearson product-moment correlation coefficient or lag-0 cross-correlation coefficient. Hanski & Woiwod (1993), however, argued that synchrony should refer to covariation in rates of change, resulting in definitions involving correlation of time series of ratios of abundance in successive years ( $R_t = N_t/N_{t-1}$ ) or differences in log-abundance ( $r_t = \log N_t - \log N_{t-1}$ ) (Steen et al. 1996, Bjørnstad et al. 1999a). The latter two address the coincidence in the direction of population change (i.e., increasing or decreasing) between two populations (Buonaccorsi et al. 2001). Practically speaking, the three measures of synchrony exhibit only slight differences in numerical behavior, but they all pertain to the same dynamical property and are fraught with similar statistical complications (reviewed below). As an intermediate between the measures of synchrony and phase synchrony, coincidence of peaks has occasionally been used as a definition of synchrony; different methods have been applied to test the significance of such

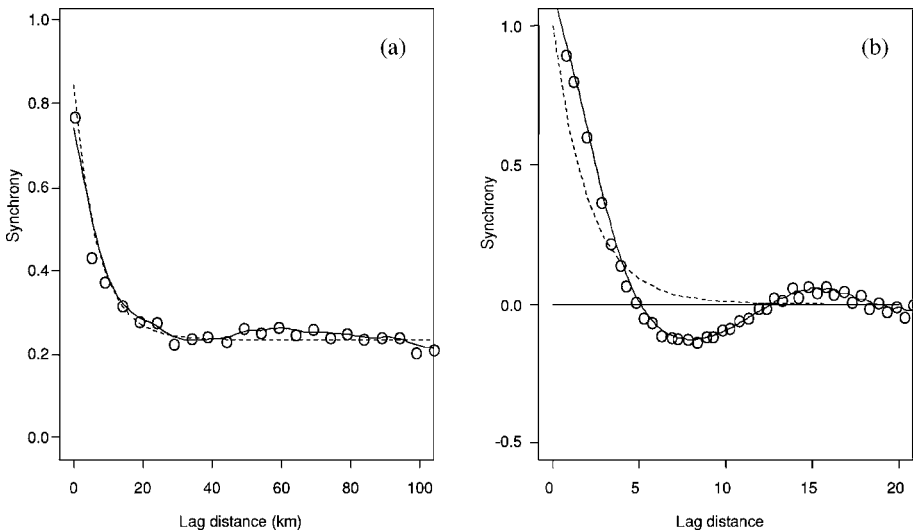
coincidence (Liebhold et al. 1996, Steen et al. 1996, Myers 1998). As a modification of this technique, phase synchrony is a powerful concept that has recently received strict definition in ecological dynamics (Haydon & Greenwood 2000, Grenfell et al. 2001, Cazelles & Stone 2003). This concept is particularly relevant for cyclic (or quasiperiodic) populations for which the relative phase in the cycle can be defined in the frequency domain by Fourier analysis (Bulmer 1975), by wavelet phase analysis (Grenfell et al. 2001) or in the time domain (Haydon & Greenwood 2000, Cazelles & Stone 2003). We first review the measures of synchrony and later turn to phase synchrony.

Given two time series of abundance, two important statistical issues must be considered. The first issue is how to handle long-term trends. The second issue is inference in the face of serial dependence, or temporal autocorrelation. In the presence of long-term trends in abundance, correlation that is due to common trends may obscure synchrony in short-term fluctuations (Buonaccorsi et al. 2001). To the extent that one is less interested in shared common trends, it may be wise to detrend the series by focusing on the residuals from a linear, polynomial, or local regression of abundance against time. For example, by detrending population densities of a bird species increasing throughout its range because of global change, the overall synchrony that is due to this trend is eliminated, and remaining synchrony, if any, is due to short-term changes in populations. Alternatively, one may use the time series of differenced log-abundances ( $r_t$ ), which explicitly focus on rates of change and for which no additional detrending is required.

A related problem is how to conduct statistical inference on synchrony given that serial dependence (temporal autocorrelation) is ubiquitous in population time series (Royama 1992). When the significance of a correlation between two time series is tested using ordinary methods, the autocorrelation violates the assumption of independence among samples (Lennon 2000, Buonaccorsi et al. 2001). "Pre-whitening," a statistical technique to remove serial dependence, has often been applied to eliminate this problem (Hanski & Woiwod 1993, Williams & Liebhold 1995, Sutcliffe et al. 1997, Paradis et al. 1999). This technique involves fitting autoregressive models to each time series, then correlating residuals from these models and conducting ordinary tests of significance. Unfortunately, by removing the autoregressive portion of these time series one may be ignoring biologically meaningful variability and synchrony (Buonaccorsi et al. 2001). Fortunately, if one has many time series, one may perform a single test for synchrony using the matrix of all pairwise correlations. For such matrices, an additional problem is that the correlation between, for example, series 1 and 2 is not independent of the correlation between series 1 and 3. However, bootstrap procedures involving resampling of locations with replacement can provide a valid test for the significance of both mean synchrony and how synchrony depends on distance (Bjørnstad et al. 1999a,b; Bjørnstad & Falck 2001). The advantage of this approach is that it does not rely on assumptions concerning independence among observations in each time series.

Technical tedium aside, a key empirical observation is how spatial synchrony often decreases as the distance between populations increases (Baars & Van Dijk

1984; Hanski & Woiwod 1993; Ranta et al. 1995a; Sutcliffe et al. 1996; Koenig & Knops 1998a; Bjørnstad et al. 1999a,b; Bjørnstad 2000, Williams & Liebhold 2000b; Peltonen et al. 2002). Various suggestions have been made for how to model this relationship between synchrony and lag distance. Of the parametric methods (i.e., methods that assume a specific functional form between synchrony and distance), the relationship has been modeled as a linear decay (Baars & Van Dijk 1984, Hanski & Woiwod 1993, Sutcliffe et al. 1996, Williams & Liebhold 2000b) or by models from geostatistical theory, such as an exponential function (Myers et al. 1995). However, because little theory exists to predict a functional form to chose (e.g., Bjørnstad & Bolker 2000), nonparametric methods that are able to capture more complex patterns of spatial correlation are often used. The two most common of these approaches is to model the relationship using smoothing splines [i.e., the nonparametric covariance function (Bjørnstad et al. 1999a,b; Bjørnstad & Bascompte 2001; Bjørnstad & Falck 2001; Peltonen et al. 2002)] or piece-wise constant 'regressograms' [cf., the modified correlogram (Koenig & Knops 1998b) or Mantel correlogram (Oden & Sokal 1986, Bjørnstad & Falck 2001)]. Figure 1 shows one parametric model and the two nonparametric methods



**Figure 1** (a) Analyses of synchrony in the Japanese wood mouse (Bjørnstad et al. 1999b) using (1) a parametric geostatistical model (*dotted line*) assuming an exponential decay to a sill (the model is  $y = 0.6 \cdot \exp[-x/6.9] + 0.25$ ); (2) The nonparametric covariance function (*solid line*), and (3) the modified correlogram (*circles*). (b) Synchrony in traveling waves in a spatially extended host-parasitoid model [both host and parasitoid dispersal rates are set to 0.7; see Bjørnstad & Bascompte (2001) for details]. Symbols are as in (a). The parametric model is  $y = \exp(-x/2.1)$ . Note how the nonparametric models are flexible enough to capture the cyclic nature of the correlation.

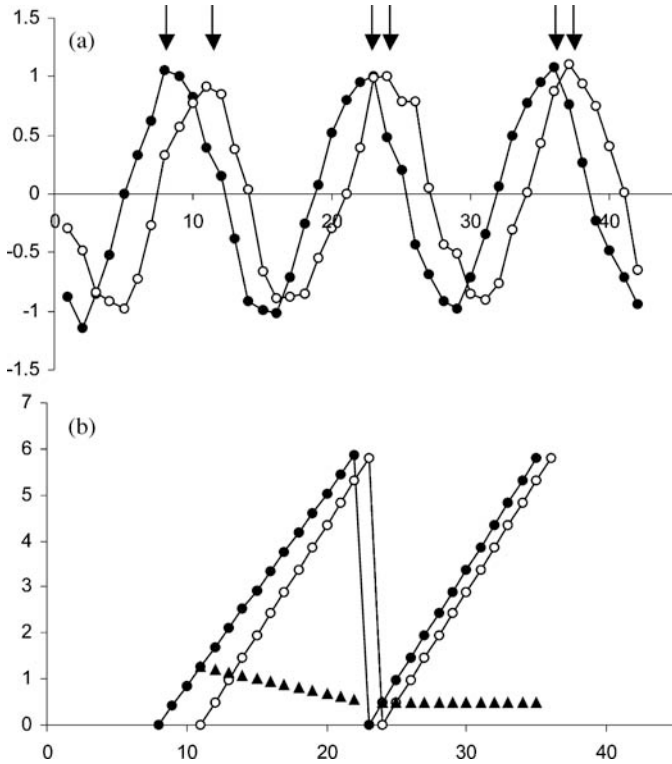
applied to the wood mice data from Hokkaido, Japan (Bjørnstad et al. 1999b), and to the traveling waves that result from spatially extended host-parasitoid models (Bjørnstad & Bascompte 2001). Bootstrap procedures are, again, useful for testing the significance of nuances in these spatial correlation functions, such as the maximum distance over which spatial synchrony extends (Koenig & Knops 1998b, Bjørnstad et al. 1999b, Bjørnstad & Falck 2001).

Approaches that focus on the correlation among series as a function of distance are in many ways analogous to the suite of geostatistical methods that quantify dependence in strictly spatial data (e.g., Rossi et al. 1992). They differ, however, in that spatial synchrony involves time and can yield absolute estimates of synchrony, whereas simple spatial autocorrelation refers to a static (nontemporal) dependence and is restricted to measuring relative synchrony. One issue that is important to both the quantification of spatial pattern in static data and to the detection of spatial synchrony in spatiotemporal data is that the scale of sampling and analysis influences the emergent patterns (Levin 1992, Dungan et al. 2002). We use the term “scale” here to refer to the magnitude of the sample unit size, the geographical extent of sampling, and the geographical resolution of the analysis. Results from one scale may not necessarily be used to draw inferences about processes operating at other scales, and therefore investigators should take care to limit generalizations from analyses to the specific scale of a study.

Correlational measures of synchrony may not always be the best representation of the synchrony-asynchrony continuum. In particular, for cyclic (or quasiperiodic) populations, subtle differences in the timing of cycles (e.g., Figure 2a) may result in low statistical correlation even when populations are closely linked. For example, the two series shown in Figure 2a appear to be superficially very correlated, yet their correlation coefficient is only  $r = 0.16$ . Visual inspection indicates a coincidence of peaks and troughs, although the series with open circles tends to lag behind the series with closed circles. For such dynamics it is useful to consider differences (or correlation) in cycle-phase rather than correlation in abundance (Haydon & Greenwood 2000, Grenfell et al. 2001, Cazelles & Stone 2003).

Such phase analysis is accomplished by transforming the time series  $N_t$  into a series of phase angles. This type of analysis is most easily illustrated by the method proposed by Cazelles & Stone (2003). They first identified the quasi-periodic maxima (e.g., arrows in Figure 2a) and then assigned phase angles,  $\theta$ , that increase linearly between 0 and  $2\pi$  as a function of time (Figure 2b). When populations are perfectly synchronized, phase differences will be near zero. However, if one series consistently lags behind the other series, then the phase differences will be consistently different from zero. Cazelles & Stone (2003) suggested a statistical test for the significance of this phase difference by comparing the frequency distribution of observed phase differences (triangles in Figure 2b) with a distribution of differences simulated for the two series under the condition of no association. However, a potential problem with the phase analysis proposed by Cazelles & Stone (2003) is that the assignment of phase angle values for each observation in a series depends entirely on identifying quasi-periodic maxima. This detail means





**Figure 2** Calculation of phase angle differences. (a) Two hypothetical time series. Arrows point to quasi-periodic maxima. (b) Phase angles of the series shown in (a). Triangles are the differences between the two series.

that most of the fluctuations between the maxima are not used in measuring phase synchrony. Furthermore, identification of maxima may be difficult if the series are not periodic or if there is a great deal of high-frequency “noise” in the system. Both of these problems may be overcome by the use of wavelet phase angles (Grenfell et al. 2001), which result from a local (in time) frequency decomposition of the time series. A further advantage of wavelet phase analyses is that one may consider multiple cycle-periods (e.g., seasonal *and* multiannual periods) and average the relative phase differences across periods (Grenfell et al. 2001).

Measures of phase synchrony provide different information about spatial dynamics than do the conventional synchrony measures (above). In theory, phase angles are unaffected by the relative amplitude of time series and they are specifically designed for detecting lags in dependence between cyclic time series. As discussed below, detection of such lags may be critical for identifying waves and other forms of complex spatial dynamics. Grenfell et al. (2001) proposed a hybrid

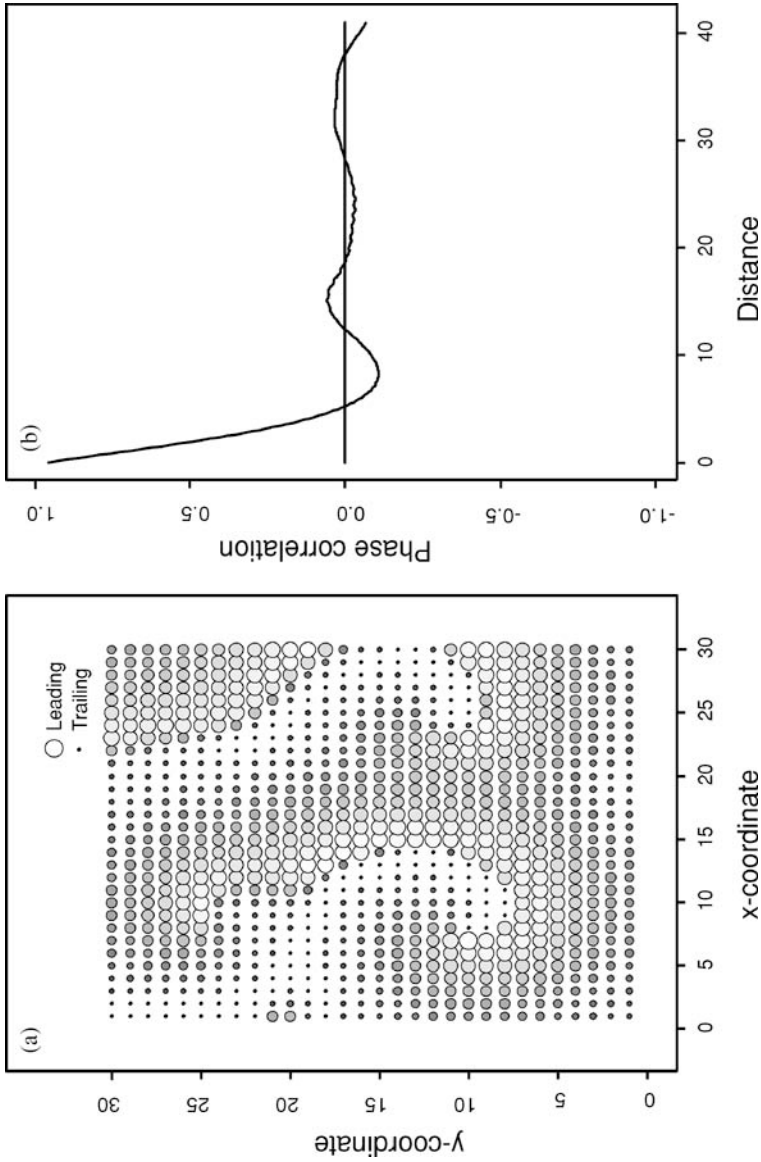
between spatial correlograms and phase analysis. Their so-called phase coherence function quantifies, in a nonparametric manner, how phase difference varies as a function of lag distance. Under this approach, all pairwise phase correlations are calculated—note here that because phases are circular, so-called circular correlations are appropriate (Jammalamadaka & SenGupta 2001)—and these phase correlations are regressed on distance. An interesting property of this function is that the increase in phase difference (i.e., the decay in phase correlation) is directly related to the speed of traveling waves. Grenfell et al. (2001) applied wavelet phase analysis to the cyclic time series of measles epidemics and found that nearby time series tended to have smaller phase differences than series located more distantly from each other. Furthermore, by analyzing how the phase difference depended on distance, they were able to map the location of apparent “foci” from which outbreaks first appeared (big cities) and spread outward at a speed of about 5 km per week.

We illustrate the wavelet phase analysis with data from the spatially extended host-parasitoid model introduced in Figure 1*b*. This model is well known to produce complex spatial dynamics such as spiral waves and spatial chaos (Hassell et al. 1991, Bascompte & Sole 1998b, Bjørnstad & Bascompte 2001). We performed simulations using this model in a  $30 \times 30$  coupled map lattice with parameters set to generate spiral waves. A movie of simulated host densities can be viewed by following the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>. Figure 3*a* shows the spatial distribution of relative wavelet phase angles (Grenfell et al. 2001) calculated from the time series on a  $30 \times 30$  lattice. The figure demonstrates the existence of several primary foci of the spiral waves. Figure 3*b* shows the phase coherence function derived from these data. The steep decay in phase coherence testifies to rapidly moving spiral waves.

## CAUSES OF SYNCHRONY

Given the frequent demonstration of population synchrony, a single cause of this behavior would be attractive. However, several possible mechanisms may cause both intraspecific or interspecific synchrony, and identifying which mechanism is more important is often difficult. The causes of population synchrony thus remain an elusive ecological question. The quest for causes is an excellent example of how simple process-oriented mathematical models can be used to test ecological hypotheses (Bascompte & Sole 1998a).

Population synchrony is closely related to a phenomenon called “phase locking” in dynamical systems theory. The existence of periodic or quasi-periodic oscillations in phenomenon ranging from animal abundance to high-speed energy waves and the prices of commodities has been recognized for hundreds of years (Huygens 1673). Phase locking between two oscillators is said to exist when  $n\phi_1 - m\phi_2 = \varphi$ , where  $n$  and  $m$  are integers,  $\phi_1$  and  $\phi_2$  are the phases of oscillators 1 and 2, and  $\varphi$  is a constant phase difference. Chaotic oscillators, in addition to periodic oscillators, may exhibit phase locking as well (Rosenblum et al. 1996).



**Figure 3** Wavelet phase analysis. (a) The relative phase differences for the  $30 \times 30$  local populations in the spatially extended host-parasitoid model from Bjørnstad & Bascompte (2001) introduced in Figure 1. A movie of simulated values can also be viewed in the Supplemental Material. Large, light circles represent leading populations. (b) The phase correlation function for the data; the steep decay in phase coherence testifies to rapidly moving spiral waves.

In either case, phase locking does not require that the amplitudes of the two series are at all the same.

When one strictly cyclic oscillator even slightly influences values of the other oscillators, phase locking may result (Rosenblum et al. 1996). Alternatively, two oscillators can be synchronized by an external source of noise or random perturbation that simultaneously affects both oscillators; even a relatively small external source may produce phase locking (Stone 1991). Similarly, theoretical models in ecology indicate that two population time series may be synchronized via direct influences such as dispersal or indirect influences such as weather or shared predation. One key conclusion is that populations may operate largely independently of each other via density-dependent processes, but a small interaction between them may be sufficient to result in synchronization. Moran (1953b) recognized this fact in his seminal paper a half century ago (below).

The role of dispersal in synchronizing populations has been studied using both autoregressive (linear) models and a variety of nonlinear population models (Barbour 1990, Holmes et al. 1994, Molofsky 1994, Ranta et al. 1995a, Haydon & Steen 1997, Kendall et al. 2000, Ripa 2000, Bjørnstad & Bascompte 2001, Kaitala et al. 2001). These studies indicate that fluctuations of any two populations that are governed by the same density-dependent process can be brought into synchrony via exchange of a small number of individuals each generation, or when populations reach their maxima. Dispersal may still synchronize populations that differ slightly in driving processes, but if the density-dependent parameters vary so much that their dynamics are vastly different (for example, if they oscillate with very different periodicity), synchronization may be difficult (Barbour 1990, Ranta et al. 1998, Swanson & Johnson 1999).

Population models can also be used to demonstrate the role of exogenous effects on synchronization. Recognition of this phenomenon is attributed to Patrick Moran, an Australian statistician whose many works include several important contributions to the theory of population ecology. Among these was a simple but profound finding that emerged from his analyses of Canadian lynx trapping records, work inspired by Charles Elton, his colleague at Oxford University (Hyde 1991). Moran (1953a,b) fit a second-order autoregressive model to the lynx time series and showed that even a small synchronous, random additive effect synchronized any two series that had identical dynamics. Furthermore, he demonstrated that the correlation between two series obeying linear (or more exactly “log-linear”) local dynamics should equal the correlation in the random effect, a mechanism that is now generally referred to as the “Moran effect” or “Moran’s theorem.” The synchronizing effect of regional stochasticity has subsequently been observed in a variety of nonlinear population models as well (Haydon & Steen 1997, Ranta et al. 1997b, Grenfell et al. 1998, Kendall et al. 2000). In most systems, the Moran effect is thought to be the result of random but synchronous weather influences acting on spatially disjunct populations (Ranta et al. 1997b; Hudson & Cattadori 1999; Koenig 1999, 2002).

Weather is not the only exogenous factor that can synchronize populations, however (Ostfeld & Keesing 2000). In some systems, mobile predators may

synchronize oscillations in spatially disjunct populations (Small et al. 1993, Ims & Andreassen 2000). Some species may be synchronized by synchronous fluctuations in populations at either lower or higher trophic levels. For example Selås and colleagues (Selås 1997, Selås et al. 2001) hypothesized that population oscillations of the herbivorous autumnal moth, *Epirrita autumnata*, are primarily determined by spatially synchronous mast seeding in their host birch trees [though serious problems with this hypothesis were recently raised (Klemola et al. 2003)]; according to this hypothesis, host foliage chemistry is more suitable for population growth in years following mast events, and synchrony of masting may thus synchronize moth oscillations. In a more complex example, synchronous masting events in oaks lead to synchronous oscillations in small mammal populations; because small mammals are the dominant predators of low-density gypsy moth, *Lymantria dispar*, populations, their synchronous oscillations may result in synchronous moth oscillations (Ostfeld & Jones 1996, Liebhold et al. 2000). Satake et al. (2004) further demonstrated that the wide-scaled synchrony in fruit production among populations of *Sorbus aucuparia* throughout southern Norway causes synchronous dynamics in both the apple moth, *Argyresthia conjugella*, which feeds on Rowan berries, and its dominant predator, the parasitoid wasp (*Microgaster politus*). Synchronous dynamics of herbivorous insects have also been suggested to cause partial spatial synchrony in insectivorous birds (Jones et al. 2003). Blasius et al. (1999) simulated the spatially extended dynamics of populations embedded in a complex food web and found that under certain conditions spatial synchrony among populations of a single species may be propagated to populations of other species in the food web [as earlier conjectured by Bulmer (1975)]. This result was extended by Cazelles & Boudjema (2001), who demonstrated a theoretical propagation of synchrony among trophically linked populations, even when their density-dependent dynamics differ. Population synchrony in any species is likely affected both by synchrony in trophically related species and by regional stochasticity, as suggested by Koenig's (2001) finding that intraspecific synchrony in North American bird species varied only slightly among seed-eating and insectivorous species.

Climatic forcing may also cause interspecific synchrony. Sympatric populations of different species sometimes exhibit synchrony even though they do not have any direct trophic interactions (Miller & Epstein 1986, Post & Forchhammer 2002, Raimondo et al. 2004). Interspecific synchrony cannot be caused by dispersal, but shared stochastic effects clearly could synchronize populations (Lindström et al. 1996, Watson et al. 2000, Post & Forchhammer 2002). We note, though, that in many systems interspecific synchrony appears to be at least partially due to the simultaneous forcing effects from shared predator population fluctuations (Ydenberg 1987, Marcström et al. 1988, Ims & Steen 1990) or the synchronizing effect of shared (Swanson & Johnson 1999) predator functional responses (Small et al. 1993). With respect to synchronized reproduction, the Moran effect also has been hypothesized to be a cause of spatial synchrony in mast seeding (Koenig & Knops 1998a; Koenig et al. 1999, 2000); however, synchronization via pollen limitation may also be capable of producing synchrony

over relatively large geographic distances (Isagi et al. 1997; Satake & Iwasa 2002a,b).

For most systems, theoretical evidence suggests that the nature of the density-dependent population processes affect the extent to which either dispersal or regional stochasticity results in synchrony. Although Moran's representation of density-dependent growth by a log-linear autoregressive model (Moran 1953b) provides useful insight into how stochasticity affects synchrony, most populations are thought to be dominated by nonlinear processes (Turchin 2003). Many nonlinear density-dependent processes may lead to a decrease in the level of synchrony predicted under linear dynamics (Allen et al. 1993; Grenfell et al. 1998, 2000; Jansen 1999; Ranta et al. 1998, 1999). However, nonlinear processes that enhance temporal periodicity may actually enhance synchrony (Ranta et al. 1998, Bjørnstad 2000). These findings are in general agreement with more theoretical studies of phase locking in nonlinear systems that indicate a close relationship between the propensity for phase locking and the Lyapunov exponent (that distinguishes asymptotically stable dynamics from cycles and chaos) (Pecora & Carroll 1990, Rosenblum et al. 1996, Earn et al. 2000).

Moran (1953b) assumed that spatially disjunct populations were governed by identical density-dependent processes. Similar assumptions are typically made when considering the synchronizing effect of dispersal (Barbour 1990, Ranta et al. 1995a). However, this assumption probably does not hold up in many systems (Swanson & Johnson 1999) because geographical variation in the population dynamics of a given species is well known (Bjørnstad et al. 1995, 1998; Henttonen et al. 1985; Williams & Liebhold 2000a). For example, Peltonen et al. (2002) demonstrated that geographical variation in gypsy moth dynamics can lead to a decrease in synchrony caused by regional stochasticity. Barbour (1990), using linear models, showed that the synchronizing effect of dispersal was largely unaffected by slight differences in dynamics. In general, however, there is limited information on how variation in dynamics affects synchronization via regional stochasticity or dispersal (Cazelles & Boudjema 2001).

Spatial variation in the habitat may also affect dispersal rates among populations in ways that affect the synchronizing effect of dispersal. For example, Bellamy et al. (2003) found that populations of certain woodland bird species were more synchronous when they were separated by forests than when they were separated by open land. Perhaps the greatest challenge to ecologists studying spatial synchrony is that the synchronizing effect of regional stochasticity is difficult to differentiate from the effect of dispersal or other synchronizing factors. In some systems, one can rule out dispersal (Williams & Liebhold 1995, Grenfell et al. 1998) or regional stochasticity (Holyoak & Lawler 1996) and thus identify the source of synchrony. But in most systems, these two phenomena co-occur, and the interaction between dispersal and regional stochasticity as causes of synchrony may not be simple; Kendall et al. (2000) found that overall synchrony was lower than would be expected by simply adding the synchrony expected from dispersal with that expected from regional stochasticity.

One approach to evaluating the overall importance of dispersal as a synchronizing agent is to compare species varying in their mobility. Analyses of breeding bird population time series from Great Britain (Paradis et al. 1999) indicated that species with greater dispersal capabilities are more highly synchronized, implicating dispersal as a major cause of the observed synchronous dynamics. Peltonen et al. (2002), in contrast, compared synchrony among six forest insect species that varied from immobile to highly mobile and found that intraspecific population synchrony showed little relation to mobility. They suggested that in these systems, regional stochasticity is a more important source of synchrony than dispersal. However, the lack of a relationship between synchrony and mobility may be due in part to the way in which complex spatiotemporal dynamics produce patterns of synchrony that greatly differ from the predictions from simple dispersal or Moran effects (Bjørnstad et al. 2002). The geographic scale of synchrony or the shape of the distance/synchrony relationship may also provide some clues as to the relative contribution of dispersal versus regional stochasticity. Sutcliffe et al. (1996) compared the geographical range of synchrony among various butterfly species that differed in their dispersal capabilities. They found that populations of more mobile species were generally more synchronous at a local (<5 km) scale but that at larger spatial scales all species were similar, exhibiting declining synchrony with distances up to ca. 200 km.

Population synchrony typically declines with the distance between populations, and most climatic variables (e.g., June maximum temperature) exhibit comparable patterns of synchrony as a function of distance (Koenig & Knops 2000, Williams & Liebhold 2000b, Peltonen et al. 2002). Determining which weather variable is a driving factor in producing population synchrony is nonetheless complicated by a typical lack of ecological understanding sufficient to finger which specific weather variable is most influential on population growth. Intriguingly, Koenig (2002) recently compared patterns of spatial synchrony in both temperature and precipitation using historical weather data collected at stations throughout the world and found that patterns varied little among different continents. This uniformity in patterns of weather synchrony may be an important explanation for the ubiquitous nature of population synchrony.

Evidence from a handful of systems suggests that synchrony may vary through time (Ranta et al. 1998, Koenig 2001) and space (Ranta et al. 1997a). Simulations using both linear and nonlinear models incorporating both dispersal and regional stochasticity indicate that this type of spatial and temporal variation in spatial synchrony can be expected as part of the self-organized properties of certain systems (Kaitala et al. 2001). However, we expect that this variation may also be due to spatial and temporal variation in the habitat, as it influences local dynamics (e.g., Liebhold et al. 2004). There is also evidence that changes in large-scale global weather patterns on a multi-decadal time scale, such as occurs in the North Atlantic Oscillation (Hurrell 1995), may affect the levels of observed spatial synchrony in animal populations (Post & Forchhammer 2002).

## SYNCHRONY AND METAPOPOPULATION PERSISTENCE

The classic concept of metapopulations refers to a collection of local populations, among which the density of individuals fluctuates independently and within which there is a reasonable chance of extinction (Harrison & Quinn 1989, Hanski & Gilpin 1991). The existence of synchrony is particularly significant to such systems because synchrony is directly related to the likelihood of global extinction (Heino et al. 1997). The more spatially synchronous a metapopulation is, the shorter its expected persistence time. The reason for this is straightforward: If all subpopulations fluctuate in unison, then when one goes extinct, all others are likely to suffer the same fate; if spatial synchrony is low, some subpopulations are likely to be abundant and serve to re-establish extinct subpopulations.

The primary mechanism responsible for this phenomenon is known as the rescue effect, and since it was first defined 25 years ago (Brown & Kodric-Brown 1977), it has been invoked as an important occurrence in a variety of systems (e.g., Sinsch 1997, Martin et al. 1997). Traditionally, the metapopulation approach has focused on species in which suitable habitats are restricted to discrete patches, but evidence suggests that a variety of species whose distributions are not subdivided in any obvious way still exhibit dynamics characteristic of metapopulations, including frequent local extinctions and recolonization from other areas. For example, in an analysis of wintering North American birds, Koenig (2001) found that local extinctions were common and that 65% of species failed to exhibit significant spatial synchrony between sites <100 km apart, a distance well within the dispersal range of most of the species. Thus, although spatial synchrony is widespread, it may nonetheless be too low to affect local extinction in many species.

The spatial distribution of habitats can profoundly affect how spatial synchrony impacts metapopulation persistence (Doak et al. 1992, Adler & Nuemberger 1994, King & With 2002). Most previous studies of the effects of spatial synchrony have found that increased synchrony leads to decreased metapopulation persistence, but increased clustering of habitat patches can potentially increase persistence by increasing the immigration between nearby patches even when dispersal is costly (Adler & Nuemberger 1994). These two factors appear to act independently of each other; that is, increased synchrony always decreases metapopulation persistence, regardless of the distribution of habitat patches, whereas increased habitat clumping appears to generally increase persistence whether the landscape is dynamic or static (Johst & Drechsler 2003).

## SPATIAL DYNAMICS BEYOND SYNCHRONY

Spatial synchrony is one manifestation among a broader array of space-time patterns. Theoretical ecologists have long demonstrated that relatively simple, non-linear, spatially explicit models are capable of generating a variety of complex



spatio-temporal patterns such as spiral waves, spatial chaos, and crystal lattices. Thus far, however, there are only a few examples of such complex spatial dynamics in natural systems. These examples include a likely “Turing patch” (comparable to a crystal lattice formation) in Western tussock moth populations (Hastings et al. 1997, Maron & Harrison 1997, Wilson et al. 1999); traveling waves in Canadian lynx populations (Ranta & Kaitala 1997, Ranta et al. 1997a, Haydon & Greenwood 2000); and recurrent waves in several host-enemy systems, including rabies (Bacon 1985, Murray 1993), measles (Grenfell et al. 2001), and larch budmoth outbreaks in the European Alps (Bjørnstad et al. 2002).

Complex spatial dynamics are generally considered to be the result of local reproduction of hosts and natural enemies coupled with dispersal (“reaction-diffusion”). Hassell et al. (1991) found that in a spatially extended Nicholson-Bailey model, certain dispersal rates yielded spiral wave dynamics. Consistent with the behavior of this model, predator-prey or host-parasitoid dynamics have been implicated in most examples of complex dynamics thus far described from field populations (Bascompte et al. 1997, Bjørnstad et al. 2002, Hastings et al. 1997, Haydon & Greenwood 2000, Wilson et al. 1999). The identification of complex spatial dynamics in nature is a considerable challenge, to no small extent because methods for identification of complex time-space patterns are in their infancy. One method involves using a directional additive model proposed by Lambin et al. (1998). A common indirect approach involves using spatial correlograms (Figure 1b). For example, Ranta and colleagues (Ranta & Kaitala 1997, Ranta et al. 1997a) used “U-shaped” correlograms as evidence for the existence of traveling waves in Canadian Lynx populations. Bjørnstad & Bascompte (2001) generated data known to exhibit various forms of complex spatial dynamics using a spatially explicit host-parasitoid model and analyzed them using spatial correlograms. Their results indicate that although the spatial correlation functions are unique, the difference between certain patterns (e.g., waves and spatial chaos) are subtle. Time-lagged correlation functions (Bjørnstad et al. 2002) or phase-coherence functions (Grenfell et al. 2001) appear to be diagnostic approaches for distinguishing among complex space-time patterns, but further method refinements and analyses of simulated data with known patterns are needed.

## CONCLUSIONS

Although the existence of spatial synchrony is often quite clear, the mechanisms behind synchrony are often murky. In the quest to identify the causes of spatial synchrony, ecological theory and models have contributed, and are likely to continue to contribute, to clarifying how endogenous and exogenous forces interact in natural populations. Clarifying the mechanisms behind spatial synchrony represents a fascinating intellectual challenge for ecologists; it also could ultimately provide critical information for understanding and managing species conservation, pest outbreaks, and disease epidemiology.

Complex spatial dynamics may well be as common as spatial synchrony in natural systems, but detecting them and understanding their causes remains a technical challenge. With the advent of new statistical methods for identifying complex spatial dynamics, we are poised at the threshold of a new era for understanding the complex interactions that drive the spatially extended dynamics of natural systems.

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