

# 6

## Spatial Synchrony of Insect Outbreaks

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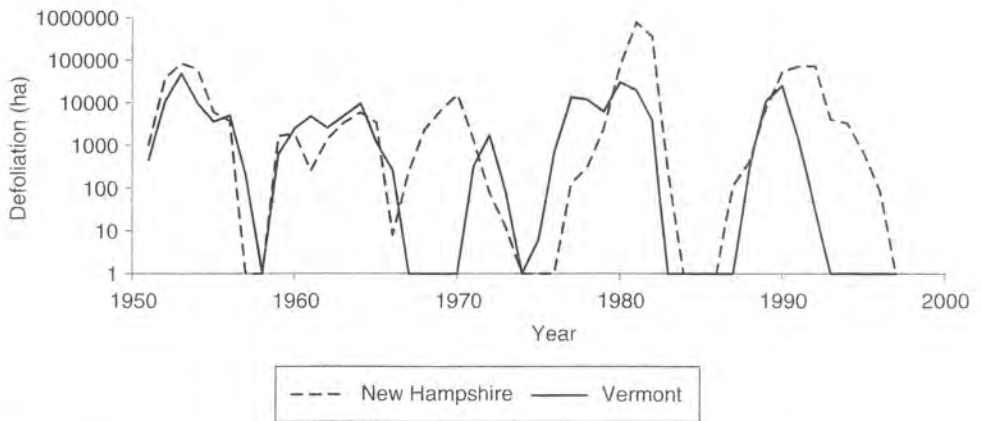
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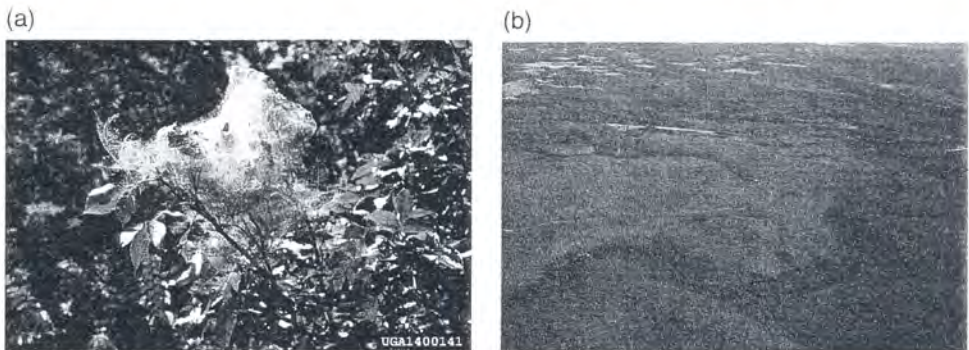
### 6.1 Introduction

The concept of “spatial synchrony” refers to the tendency of the densities of spatially disjunct populations to be correlated in time (Bjørnstad *et al.* 1999a, Liebhold *et al.* 2004). Outbreaking forest insects offer many of the classic examples of this phenomenon (Figure 6.1). The spatial extent of synchrony of outbreaks is probably one of the most important – yet most underappreciated – characteristics that cause certain insect species to be classified as noxious pests. Locally eruptive population behavior alone would rarely qualify a species for “outbreak” status. Rather, regionalization of eruptions is what elevates ecological and socioeconomic impacts of certain species to high levels of concern, which gives them pest status. Consider for example the contrast between the fall web worm, *Hyphantria cunea*, and the gypsy moth, *Lymantria dispar* (Figure 6.2). The former can reach very high localized densities and denude branches of leaves, but in North America this defoliation is typically limited to isolated colonies on different branches on different trees over several years. Due to the highly localized nature of its damage, this species is not considered a major pest in the eastern United States. The gypsy moth in contrast is considered a highly noxious species because its defoliation is extremely synchronized, extending continuously over thousands of hectares in a single year.

Outbreaks of forest insects can have vast impacts on ecosystem functions. These effects include nitrogen leaching, carbon sequestration, and alteration of fire regimes (McCullough *et al.* 1998, Lovett *et al.* 2002, Schowalter 2011). There is a



**Figure 6.1** Spatial synchrony in gypsy moth populations. Time series of annual area defoliated by the gypsy moth, *Lymantria dispar*, in two adjacent states in the United States, 1951–2008. Defoliated area serves as a proxy for regional population density. Note the general temporal coincidence of both peaks and troughs in the time series.



**Figure 6.2** Contrast between regionally synchronized and unsynchronized outbreaks. (a) defoliation caused by *Hyphantria cunea* (photo: Linda Haugen, USDA Forest Service, Bugwood.org); due to the highly localized nature of its damage, this species is not considered a major pest in the eastern United States. (b) Extensive defoliation caused by *Lymantria dispar* (photo: Karl Mierzejewski, Centre Co., PA); due to the synchronous occurrence of high densities over large areas, this species is considered a major pest species in the eastern United States.

critical spatial component to all of these impacts. For example, the consequences of outbreak-caused elevated nitrogen leaching on stream chemistry are much more pronounced when outbreaks occur simultaneously over an entire watershed (Eshleman *et al.* 2004). There is also a strong (though poorly studied) relationship between spatial synchrony of insect outbreaks and socioeconomic impacts. For example, widespread forest defoliation and tree mortality are more likely to result in a loss of scenic value and tourism revenues (Lynch and Twery 1992). Similar spatial properties characterize the economic effects of outbreak synchrony on agricultural and timber values. Forest disturbances, such as bark beetle outbreaks, that



extend over large areas often result in a depression of timber prices created by excessive supply generated from salvage harvest (Holmes 1991). Prices of agricultural commodities often rise as a result of widespread insect outbreaks that cause drops in supply and/or cause increases in production costs (Hoddle *et al.* 2003).

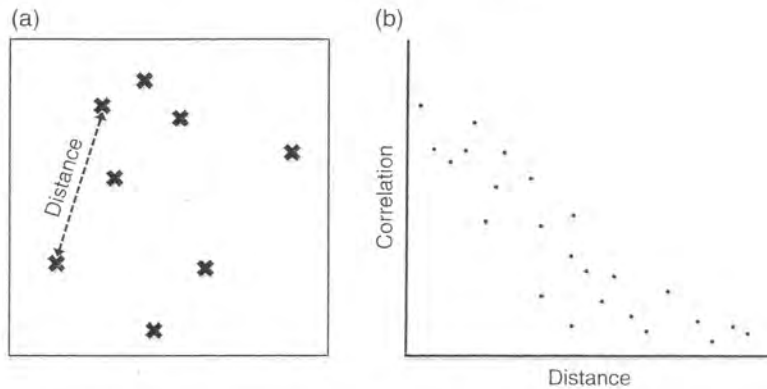
## 6.2 Quantifying synchrony

Spatial synchrony and the resultant regionalization of outbreak dynamics have been measured in many ways. The simplest and most common approach is to use the Pearson product-moment correlation among pairs of spatially disjunct time series of local abundance (Bjørnstad *et al.* 1999a, Buonaccorsi *et al.* 2001, de Valpine *et al.* 2010). Very often, however, data on local insect abundance are not available. In such cases, records of outbreak incidence and severity (e.g., defoliation) over time are used as proxies for abundance. While the resulting time series of outbreak incidence may fail to capture the detailed variations in abundance, particularly those that occur at sub-outbreak levels, such data tend to be reasonably correlated with true population densities and thus provide adequate proxies for assessing synchrony (e.g., Bjørnstad *et al.* 2002).

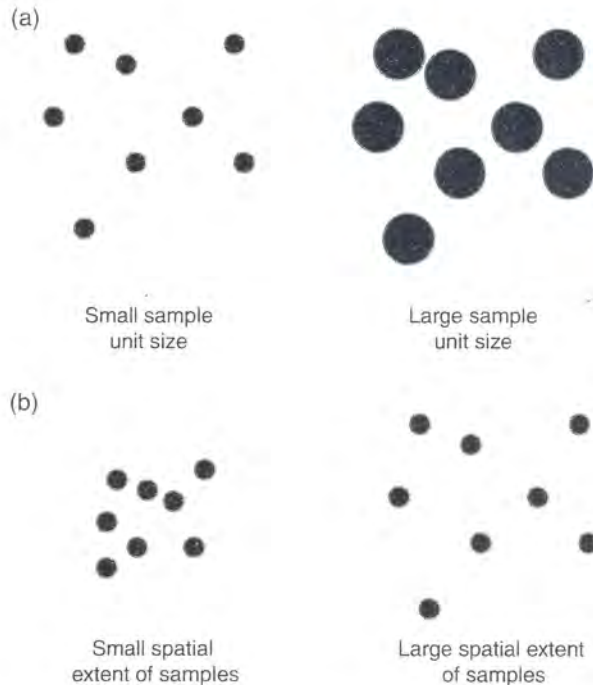
Spatial synchrony cannot be understood or quantified without reference to spatial scale because synchrony typically depends on the distance between locations (Liebhold *et al.* 2004, Fox *et al.* 2011). The maximum geographical extent over which synchrony extends varies among species and locations (Hanski and Woiwod 1993, Peltonen *et al.* 2002), but often extends over several hundred kilometers in forest insects (Peltonen *et al.* 2002). Quantifying the relationship between synchrony and distance is valuable because it can provide critical information, not only about the consequences of synchrony but also about its causes (Bjørnstad *et al.* 1999a, b). For example, differentiation among possible mechanisms driving observed synchrony can be accomplished by comparing the scale of synchrony in data simulated using alternate mechanistic models. However, it is often difficult to infer process from pattern because very different processes can lead to similar patterns of spatial dynamics.

When many georeferenced time series are available, it is useful to calculate all pairwise correlation coefficients between them and examine how the correlation depends on spatial distance (Figure 6.3). In most biological systems, cross-correlations decline with increasing distance between sampling locations (Liebhold *et al.* 2004, Fox *et al.* 2011, but see Ranta and Kaitala 1997, Bjørnstad and Bascompte 2001 for exceptions to this rule). The spatial scale of synchrony is usually measured as either the distance at which cross-correlations decline to zero or to the region-wide average correlation (Bjørnstad *et al.* 1999a, b). Several related statistical methods are available for characterizing the relationship between synchrony and distance. Many of these, including Koenig's (1999) modified correlogram and the nonparametric spatial covariance function (Bjørnstad and Falck 2001), are implemented in the NCF package of the R statistical program (R Development Core Team 2010).

When sampling to quantify synchrony, it is important to consider the spatial extent of the sample, that is, the size of the region over which synchrony is investigated, and the spatial extent and spacing of the individual sample units



**Figure 6.3** Illustration of a hypothetical time series correlogram. (a) Irregular spatial configuration of sample locations for eight population time series. (b) Time series correlogram of hypothetical data displays the correlation coefficient calculated between each pairwise combination of time series versus the distance between sample locations.



**Figure 6.4** Two aspects of scale in sampling spatial synchrony. Black circles represent the sample area for time series. (a) Varying the sample unit size for each sample. (b) Varying the spatial extent among sample locations.

(Figure 6.4). The spatial extent of the sample unit can greatly influence the quantification of synchrony. Fluctuations in abundance in small sampling areas may be dominated by local stochasticities in dynamics as well as observational errors when densities are low that may distort both patterns of synchrony. As the

sample unit size increases, patterns of synchrony may become clearer, though sometimes this clarity comes at the cost of diluting the synchrony versus distance signal (Bjørnstad and Falck 2001). This phenomenon is not limited to insect outbreaks or even to ecological data, and is a widely recognized phenomenon referred to as the “modifiable areal unit problem” in geography in which the shape and/or size of the units on which data are mapped can change the resulting correlations or statistical models generated from the data (Openshaw 1984, Wu 2004). If the spatial extent of the study is small, one may fail to quantify the scale of synchrony because it might be larger than the greatest distances considered. Similarly, if the spatial extent is large but the number of sample units is small, one may fail to quantify the scale because it may be smaller than the shortest distance among widely spaced samples.

### 6.3 Causes of spatial synchrony

Despite the ubiquity of spatial synchrony in forest insect outbreaks, its causes are often difficult to identify because of the general “inverse problem” of inferring process from pattern – very different processes can lead to similar dynamic patterns (Nelson *et al.* 2004). There are multiple potential causes of spatial synchrony: dispersal, regional stochasticity, and trophic interactions (Bjørnstad *et al.* 1999a, Liebhold *et al.* 2004). Moreover, all of these forces act simultaneously, but with varying importance in different insect species.

#### 6.3.1 Dispersal

Mathematical models show that the density-independent exchanges of even a small number of individuals among spatially disjunct populations can lead to synchrony (Barbour 1990, Bjørnstad and Bolker 2000, Liebhold *et al.* 2004). In highly mobile species, dispersal might be expected to lead to synchronous dynamics across large regions. However, population synchrony has been observed over large distances even among totally isolated populations (Grenfell *et al.* 1998, Ims and Andreassen 2000). Moreover, a comparison of spatial synchrony among six forest insect species revealed that there was little relationship between a species’ dispersal ability and the distances over which populations are synchronous (Peltonen *et al.* 2002). An extreme example is provided by the gypsy moth in North America; adult females are completely flightless, yet defoliation records indicate that populations are synchronous across distances of 600–900 km (Peltonen *et al.* 2002, Haynes *et al.* 2009) (Figure 6.1).

A further complication is that the ability of dispersal to induce synchrony appears to be highly dependent on the relationship between dispersal and density. Most theoretical studies indicating dispersal as a synchronizing force assume a density-independent dispersal rate. However, Ims and Andreassen (2005) demonstrated experimentally and theoretically that dispersal is not an important synchronizing agent when dispersal is negatively density dependent (i.e., when the dispersal rate is highest from low-density populations). In contrast to positive density-dependent dispersal, which would tend to force the densities of subdivided populations toward a regional average, negative density-dependent dispersal



would tend to inflate differences in density among populations as individuals would move from low-density populations and settle in high-density populations. Negative density-dependent dispersal is common in a variety of taxa, perhaps due to the difficulty of finding mates or avoidance of inbreeding in low-density populations (Hanski 1999, Ims and Hjermmann 2001, Clobert *et al.* 2004).

### 6.3.2 Regional stochasticity

Moran (1953) showed that stochastic density-independent factors – such as precipitation or temperature anomalies that are correlated across great distances (see Koenig 2002, Peltonen *et al.* 2002) – can drive population synchrony across large regions. Specifically, Moran showed that the correlation of two populations exhibiting identical log-linear population dynamics should equal the correlation in the stochastic factor affecting both populations. In the following decades, the ability of this process, known as the “Moran effect” or “Moran’s theorem” (Royama 1992), to synchronize populations across regional scales has been explored extensively in both theoretical and empirical studies (e.g., Grenfell *et al.* 1998, Bjørnstad *et al.* 1999b, Hudson and Cattadori 1999, Koenig 2002, Peltonen *et al.* 2002). Regionally correlated random factors, particularly weather, have been widely accepted as a major driver of observed patterns of population synchrony (reviews in Bjørnstad *et al.* 1999a, Liebhold *et al.* 2004).

Moran (1953) showed that the regionally stochastic effect may exert a relatively weak effect on change in abundance compared to density-dependent effects but still have a strongly synchronizing effect. Because these synchronizing stochastic effects may be small, it often is difficult or impossible to isolate their identity, though there are a few examples where information on this has been inferred. For example, outbreaks of the spruce budworm in eastern Canada may be synchronized by spatial correlation in the recruitment rate of eggs resulting from dependence of the recruitment rate on weather conditions (Royama *et al.* 2005).

Moran’s (1953) original work assumed that all subpopulations were governed by identical density-dependent processes. Peltonen *et al.* (2004) and Liebhold *et al.* (2006) used the same second-order autoregressive population model used by Moran (1953) to show that population synchrony generated through synchronous variability in weather may be weakened by geographic variability in the strength of density dependence. Furthermore, considerable geographic variation in density dependence and population behaviors (e.g., outbreak frequency and periodicity) has been observed in a variety of species (Johnson *et al.* 2006, Cooke and Lorenzetti 2006, Peltonen *et al.* 2004). In the two-year cycle spruce budworm, *Choristoneura biennis*, for example, regional synchrony of outbreaks appears to be reduced due to geographic variation in population dynamics associated with local differences in forest stand characteristics (Zhang and Alfaro 2003).

Moran (1953) also assumed that the dynamics of synchronized populations followed a second-order log-linear model, but such assumptions of linearity are not realistic for most forest insects (Turchin 2003). Nonlinearities in density-dependent population growth can greatly influence population synchrony.

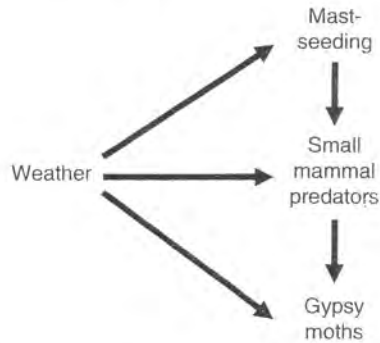
Whereas the synchrony of populations governed by linear dynamics equals the synchrony of environmental perturbations (Moran 1953), nonlinear density dependence can cause population synchrony to be substantially greater or lower depending on the type of population behavior exhibited (e.g., cycles or chaos) (Grenfell *et al.* 1998, Ranta *et al.* 1998, Bjørnstad 2000). Nonlinearities producing cyclic dynamics enhance population synchrony through nonlinear phase locking (Bjørnstad 2000). In this process, exchange of very few individuals between populations will bring populations into synchrony (Bjørnstad *et al.* 1999a, Jansen 1999). Moreover, phase locking may produce synchrony over distances much greater than the dispersal distances of individuals (Jansen 1999).

### 6.3.3 Trophic interactions

Probably the best understood examples of food web interactions leading to population synchrony involve microtine rodent populations synchronized by nomadic predators; avian predators concentrate in patches of high prey density moving prey densities in these patches to levels more similar to the regional average (Ydenberg 1987, Ims and Steen 1990). Many natural enemy species are highly mobile, and orient toward areas of locally high prey population densities, resulting in spatial density dependence in their effects on host populations (Walde and Murdoch 1988). Such spatial density dependence is sometimes capable of stabilizing host populations (Hassell and May 1973, Murdoch and Stewart-Oaten 1989). Although synchrony in forest insect populations has not been directly linked to mobile predator populations, some findings suggest that this possibility warrants further consideration. In particular, Barber *et al.* (2008) found that cuckoos, which are known to exploit insect outbreaks, concentrate in areas of gypsy moth outbreaks. Parasitoids of forest insects are known to aggregate into areas of high-host density (Liebhold and Elkinton 1989, Gould *et al.* 1990, Parry *et al.* 1997); however, the dispersal capacity of parasitoids may be too low to synchronize hosts over regional scales though they may lead to local synchrony. Though it has received less attention, mobile insect pathogens could similarly serve to synchronize host populations. However, in the case of entomopathogenic viruses, movement of these pathogens is likely insufficient to influence the synchrony of forest insects across large regions (Abbott and Dwyer 2008).

In recent years, there has been growing recognition of a broader role of food web interactions in population synchrony. Traditionally, Moran effects are thought to be caused by the direct action of weather on the survival or reproduction of individual species. It is becoming increasingly clear that exogenous effects can indirectly synchronize the fluctuations of a given species by increasing the synchrony of resource or consumer species (Cattadori *et al.* 2005, Haynes *et al.* 2009). In the northeastern United States, large-scale resource pulses provided by mast seeding of oaks are a major driver of population cycles of the white-footed mouse (Wolff 1996, McShea 2000, Elias *et al.* 2004, Clotfelter *et al.* 2007, Schmidt and Ostfeld 2007), which prey opportunistically on gypsy moths (Smith 1985; Yahner and Smith 1991). Synchrony in white-footed mouse populations resulting from mast seeding of their primary winter food source, red-oak acorns, has been hypothesized to help synchronize gypsy moth populations (Ostfeld and





**Figure 6.5** Interactions by which stochasticity in weather contributes to synchrony among gypsy moth populations (Haynes *et al.* 2009). Weather may cause direct synchronized stochastic effects (e.g. extreme cold temperatures may cause mortality in certain life stages). In addition, weather may act indirectly to cause synchronized stochasticity in gypsy moth populations by altering mast seeding or small mammal predator populations.

Jones 1996, Liebhold *et al.* 2000). Haynes *et al.* (2009) recently found that red-oak acorns, white-footed mice, and gypsy moths display similar levels of spatial synchrony over comparable distances. They also found that a mechanistic model of interactions among these species (as well as a specialist viral pathogen of the gypsy moth) indicated that regional synchronization of mast seeding through climatic forcing could indirectly synchronize the fluctuations of the white-footed mouse and gypsy moth (Figure 6.5). Similar mast-induced synchrony that trickles down the trophic chain has been documented in the apple fruit moth, *Argyresthia conjugella*, and its parasitoid, *Microgaster politus* (Satake *et al.* 2004).

It is often difficult to sort out the causes from the consequences of herbivore outbreak synchrony on higher trophic levels. Little information is available about the effects of herbivore spatial synchrony on populations at higher trophic levels (but see Satake *et al.* 2004). We can perhaps infer from the literature on mast seeding in plants (Silvertown 1980, Kelly and Sork 2002) that spatial synchrony in prey insect oscillations can satiate predator and parasitoid populations and thereby limit their ability to regulate hosts via spatial density dependence. Thus, spatial density dependence in the response of predators and parasitoids may contribute to the synchronization of host populations, but spatial synchrony in host populations may adversely affect the same spatial density dependence of higher trophic level impacts.

#### 6.4 The ubiquity of synchrony and its implications

The presence of spatial synchrony in population dynamics in nearly every major taxa (Liebhold *et al.* 2004) begs the question: why is population synchrony so ubiquitous? The most likely explanation is that weather appears to co-vary through time in a similar fashion at continental scales across all parts of the Earth (Koenig 2002). All species may disperse at some – albeit often quite



limited – observable scale. The lack of relationship between dispersal ability and spatial extent of population synchrony, even among forest insects with similar population dynamics (Peltonen *et al.* 2002), suggests dispersal may not explain the pervasiveness of population synchrony. Although weather may be the dominant force underlying population synchrony, the relationship between weather and population synchrony is probably almost never as simple as predicted by Moran's (1953) theorem. Spatial heterogeneities and nonlinearities in population dynamics both can modify the synchronizing effects of weather on populations. Furthermore, the synchrony of a target species can be synchronized by spatially correlated weather both directly (e.g., through weather-induced mortality) and indirectly due to propagation of synchrony through trophic chains (Satake *et al.* 2004, Cattadori *et al.* 2005, Haynes *et al.* 2009) (Figure 6.5).

Understanding the causes of outbreak synchrony has important implications for how insect populations are best managed. Specifically, if synchrony is primarily caused by dispersal, then suppression of outbreaks can be expected to have a positive impact on preventing outbreaks in neighboring areas. The concept of dispersal-driven synchrony is closely related to the "epicenter hypothesis," namely, that outbreaks start in specific areas and that outbreaks in neighboring areas are triggered by immigration from epicenters; this concept has been advanced to describe the spatial dynamics of several different forest insects such as the gypsy moth and spruce budworm, but evidence for the concept is sparse (Liebhold and McManus 1991, Royama 1992, Johnson *et al.* 2004). Implicit to the epicenter hypothesis is the existence of multiple stable equilibria and massive levels of dispersal, neither of which are well documented in most forest insect species. Given the questionable status of the epicenter hypothesis and the overall dominant role of weather (acting either directly or indirectly via trophic interactions) as the driving force behind spatial synchrony in insect outbreaks, there seems to be little justification for pro-actively suppressing "epicenters" in order to prevent outbreaks from spreading to adjoining areas.

While the ubiquity of spatial synchrony in insect outbreaks is remarkable, care should be taken in characterizing the extent of synchrony. Examples of what we feel are exaggerations of spatial synchrony include studies by Myers (1998) and Hawkins and Holyoak (1998), who reported synchrony of outbreaks extending over thousands of km, sometimes among continents. Synchrony in interannual variation in weather generally does not extend over such massive distances (Koenig 2002), and thus it is difficult to comprehend how a Moran effect could explain such extreme spatial extent of synchrony. Johnson *et al.* (2005) provide a detailed description of the failure of Myers (1998) and Hawkins and Holyoak (1998) to account for spatial autocorrelation in time series and how this may have negated the statistical analyses upon which they based their conclusions. We believe that a similar problematic application of statistical tests of correlation that neglect inherent temporal autocorrelation can be found in Selås *et al.* (2004), who proposed that forest insect outbreaks may be synchronized indirectly by low sunspot activity, which would result in global synchrony. The authors reasoned that UV-B radiation from the sun peaks in periods of low sunspot activity, causing trees to respond by increasing the production of UV-B protective phenolics at the expense of production of secondary compounds for herbivore resistance. This is

a creative idea but we believe that, like Hawkins and Holyoak (1998) and Myers (1998), Selås *et al.* (2004) failed to account for temporal autocorrelation in insect and sunspot data and consequently reached a spurious conclusion.

The classic perspective on population synchrony is that it is a characteristic but not a cause of population fluctuations. This is perhaps most clearly embodied in the Moran theorem that effectively establishes that the mechanisms responsible for synchronizing populations may be completely independent of the mechanisms responsible for regulating populations (Moran 1953). With respect to outbreak ecology, this perspective implies that synchrony may be important because it exacerbates the economic burden and strains the logistical abilities of management agencies to mitigate impacts. An alternative perspective, however, is that synchrony plays a much more integral, causal role in outbreak ecology (Bjørnstad *et al.* 2008). The idea is that synchrony results in regionalization of population fluctuations and this regionalization dilutes the regulating abilities of mobile natural enemies that would otherwise provide control of local eruptions. Synchrony, then, may be a critical cause of outbreaks.

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