Synchronized Dynamics of *Tipula paludosa* Metapopulation in a Southwestern Scotland Agroecosystem: Linking Pattern to Process

Daniel Bearup,1 Sergei Petrovskii,1,* Rod Blackshaw,2 and Alan Hastings3

1. Department of Mathematics, University of Leicester, University Road, Leicester LE1 7RH, United Kingdom; 2. Centre for Agricultural and Rural Sustainability, University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom; 3. Department of Environment Science and Policy, University of California, Davis, California 95616

Submitted November 5, 2012; Accepted February 22, 2013; Electronically published July 12, 2013

Online enhancement: appendix.

**Abstract:** Synchronization of population fluctuations at disjoint habitats has been observed in many studies, but its mechanisms often remain obscure. Synchronization may appear as a result of either interhabitat dispersal or regionally correlated environmental stochastic factors, the latter being known as the Moran effect. In this article, we consider the population dynamics of a common agricultural pest insect, *Tipula paludosa*, on a fragmented habitat by analyzing data derived from a multiannual survey of its abundance in 38 agricultural fields in southwestern Scotland. We use cross-correlation coefficients and show that there is a considerable synchronization between different populations across the whole area. The correlation strength exhibits an intermittent behavior, such that close populations can be virtually uncorrelated, but populations separated by distances up to approximately 150 km can have a cross-correlation coefficient close to one. To distinguish between the effects of stochasticity and dispersal, we then calculate a time-lagged cross-correlation coefficient and show that it possesses considerably different properties to the nonlagged one. In particular, the time-lagged correlation coefficient shows a clear directional dependence. The distribution of the time-lagged correlations with respect to the bearing between the populations has a striking similarity to the distribution of wind velocities, which we regard as evidence of long-distance wind-assisted dispersal.

**Keywords:** metapopulation, synchronization, dispersal, Moran effect, *Tipula paludosa*.

**Introduction**

Understanding of population dynamics in complex environments has been one of the main challenges for both theoretical and empirical ecology over the last few decades (Levin 1976; Kareiva 1990; Lundberg et al. 2000). Environment is known to shape the geometry of ecological interactions through a variety of specific spatial and spatiotemporal mechanisms, such as landscape structure (Pickett and Thompson 1978; Kaitala et al. 2001), seasonality and solar cycles (Sinclair and Gosline 1997), and transient weather conditions on both global and regional scales (Baars and Van Dijk 1984; Post and Forchhammer 2002; Raimondo et al. 2004). The latter is usually regarded as environmental stochasticity or noise (see Vasseur and Yodzis 2004 and references therein).

Landscape heterogeneity often results in a situation in which populations of the same species occupy disjoint habitats. Depending on the interhabitat distance, individual mobility, and the nature of the environment between the habitats (e.g., how harsh it is), these local populations may or may not interact with each other through dispersal. The classic concept of metapopulation (Hanski and Gilpin 1991) refers to the case in which the sizes of local populations fluctuate independently, thus assuming that the dispersal coupling between them can be neglected. In many cases, however, this is not the case, and the population fluctuations in different habitats appear to be, to a certain extent, correlated (so that the metapopulation concept had to be updated accordingly; Haydon and Steen 1997; Sutcliffe et al. 1997). This phenomenon is known as synchronization, and interhabitat dispersal has been identified as a synchronizing factor (Liebhold et al. 2004). There is considerable evidence that dispersal coupling by just a tiny fraction of the population may bring population fluctuations into synchrony (Haydon and Steen 1997; Kendall et al. 2000; Ripa 2000).

Remarkably, dispersal coupling is not the only factor resulting in population synchronization. The impact of spatially correlated environmental noise on disconnected populations can also synchronize the population fluctuations; this phenomenon is known as the Moran effect (Moran 1953a, 1953b; Royama 1992; Ranta et al. 1997). Having
originally been discovered theoretically (cf. “Moran’s theorem”), it has later been widely observed in different taxa and in various environments (Liebhold et al. 2004). Synchronization of population fluctuations can therefore be driven by the regional environmental stochasticity, by the interaction between local populations through dispersal, or by a mixture of both (Goldwyn and Hastings 2011). Without any impact from the Moran effect, dispersal is typically too weak a force to produce synchrony (Goldwyn and Hastings 2011), but the Moran effect alone cannot produce very high levels of synchrony. What is less clear is the relative importance of these two forces.

Synchronization has many implications across the whole range of ecological sciences. A good understanding of patterns and mechanisms of synchronization is required to efficiently manage issues arising in agroecology (Rosenstock et al. 2011), in pest control (Milne et al. 1965; Blackshaw 1983; Williams and Liebhold 1995), and in nature conservation programs (Earn et al. 2000). Identifying particular factor(s) resulting in synchronization is therefore important. Indeed, linking an observed ecological pattern to a specific process has been a major issue in contemporary ecology (Levin 1992). However, because both dispersal and the Moran effect can have a similar impact on population dynamics, it is often very difficult to distinguish between them unless direct measures of the effect of dispersal are possible. For example, observed synchronies in the yield of pistachio trees must be due only to the Moran effect, because there is no equivalent to dispersal in this system, and this is confirmed by models (Lyles et al. 2009). However, a system in which dispersal can be eliminated as a force causing synchrony is rare, and differentiating the effects of stochasticity from those of dispersal is sometimes regarded as one of the greatest challenges to ecologists studying spatiotemporal population dynamics (Liebhold et al. 2004).

Another challenging problem is to identify the corresponding spatial scale of the mechanisms involved. For species with low mobility, the scale of synchronization attributable to dispersal is known to be smaller than the scale induced by the regional stochasticity. In particular, in a field study of butterflies, Sutcliffe et al. (1996) showed that the spatial scale of dispersal coupling is on the order of 5 km, whereas population synchrony can be observed at much larger distances of up to 200 km. The larger spatial scale of synchronization is therefore likely to be linked to regional stochasticity, although this may not always be true if insect dispersal is assisted by the wind. Synchronization of population dynamics has been observed for many other insect species (Baars and Van Dijk 1984; Hanski and Wolff 1993; Sutcliffe et al. 1996; Peltonen et al. 2002), although the specific factors responsible for synchronization were not always clear. Other striking examples of patterns of synchrony come from the dynamics of childhood diseases (Rohani et al. 1999). This study shows the importance of interactions between dispersal and dynamics, because two diseases, measles and pertussis, show very different spatiotemporal patterns, even though the dispersal parameters must be the same.

In this article, we consider how the spatial pattern observed in population dynamics of an insect species dwelling on a habitat consisting of an array of agricultural fields can be affected by the landscape properties and by the weather conditions. The focus of this study is on Tipula paludosa, which is a common pest in the British Islands that can cause significant damage to agriculture (Blackshaw and Coll 1999). For this reason, its dynamics have been a focus of numerous field studies (Milne et al. 1965; Mayor and Davies 1976; Blackshaw 1983) as well as some theoretical work (Blackshaw and Petrovskii 2007).

To address the issues of pattern, process, and scale, we have analyzed annual data on the population abundance of T. paludosa collected between 1980 and 1994 in a few dozen agricultural fields across southwestern Scotland. Analysis of the time series of population density obtained at different locations across the region shows that the fluctuations in the abundance of T. paludosa are not independent. However, the synchronization pattern that we have observed exhibits some rather counterintuitive properties. There is a considerable degree of synchronization between some of the fields but an absence of synchronization between others. Note that the generic dependence of synchronization on the interhabitat distance is well known, with the degree of synchronization between different populations usually decreasing with distance (Sutcliffe et al. 1996; Lundberg et al. 2000; Liebhold et al. 2004). However, contrary to this, synchronization between T. paludosa abundances in different fields does not show any clear relation to the interfield distance. Furthermore, we show that the observed synchronization pattern has a distinct directional aspect. In particular, although the northwestern and southeastern areas of the region are, on average, strongly correlated, there is much less correlation between the northeastern and southwestern areas. By linking this directional asymmetry to weather data, we show that it is likely to result from wind-assisted dispersal. To distinguish the effect of dispersal from that of stochasticity, we introduce a delay-based cross-correlation coefficient and show that it exhibits a pattern of directional dependence very similar to that of the wind velocity.

Methods

Species

Tipula paludosa Meigen, the marsh cranefly, is found in cool temperate regions of northern Europe and the United
Synchronized Dynamics of T. paludosa

The purpose of this study is to investigate the synchronization of local populations (i.e., the populations in individual fields). To obtain a detailed view of the spatial aspect, it is desirable to include as many fields as possible. On the other hand, the accuracy of estimates of the degree of synchronization will be dependent on the length of the time series used. Consequently, it is preferable both that time series cover the greatest duration possible and that as many different time series as possible are used.

Given these limitations, it is not possible to use all fields surveyed. A compromise between number of fields and length of time series has to be found. Consequently, we restrict our analysis to a subset of 38 fields for which a complete 15-year time series between 1980 and 1994 is available. A map of the fields in question can be seen in figure 1.

Information about the minimum, maximum, and time-average size for each of the local populations (as represented by the mean value across the collected soil cores; see above) is given in table 1. It is readily seen that the populations exhibit considerable variability. More detailed data on the T. paludosa population size in five particular fields over the given period, 1980–1994, are shown in figure 2. A visual inspection of the data reveals a certain degree of correlation between the time series, such as a decrease in all five population sizes between 1987 and 1988, a minimum population size in 1985 and 1993 (three of five fields), an increase in the population size between 1993 and 1994 (four of five fields), and so on. A quantitative insight into this is made below.

Elimination of Population Density Dependence

Ninety-seven percent of the populations included in the study (37 of 38 fields) display significant population density dependence when subjected to the test outlined by Pollard et al. (1987). The effects of this density dependence on local population dynamics may obscure the effects of synchronization between these populations. Consequently, it is desirable to eliminate these density-dependent effects from the local population dynamics.

To describe the density effects in T. paludosa dynamics, the following model,

\[ \Delta N_t = N_{t+1} - N_t = N_t \left[ 10^{\alpha \frac{N_t}{\bar{N}} - \beta} - 1 \right], \]  

(1)

(where \( \bar{N} \) is the average population across the entire study area, and \( \alpha \) and \( \beta \) are to be determined), which we write as

\[ N_{t+1} = f(N_t) = N_t \cdot 10^{\alpha \frac{N_t}{\bar{N}} - \beta}, \]  

(2)
was derived by Blackshaw and Petrovskii (2007) from regression of per capita growth rate versus relative abundance. The parameters $\alpha$ and $\beta$ can be determined by linear regression of $\log \left( \frac{\Delta N_i}{N_i} + 1 \right)$ against $\log \left( \frac{N_i / N}{H_{11001}} \right)$ for a given time series. Density dependence is expected to be a species property, and as such, the same parameters apply for each individual population. Thus, we determine these parameters for the time series obtained by computing the average population across all fields at each time point. The resulting data are plotted in figure 3. Note that the resulting values of $\alpha$ and $\beta$ correspond well to those obtained in earlier studies (Blackshaw and Petrovskii 2007).

Now, for each time series of populations, $X$, we can compute the difference between the observed and predicted populations for any time point as follows:

$$R^X_i = X_i - f(X_{i-1}),$$

(3)

(where $t = 2, 3, \ldots, n$) to obtain a time series of residuals, $R^X$, one time step shorter than the original observed data. These residuals measure the degree to which real populations deviate from the levels predicted by the density-dependent mechanism, either by chance or because of underlying processes that are not described by internal population regulation.

A histogram of all such residuals was constructed (fig. 4) that strongly suggested that the residuals arise from a lognormal distribution. To confirm this intuition, a Q-Q
Finding Relationships between the Local Populations

We quantify the degree of synchronization between the populations of two fields (e.g., \(X\) and \(Y\)) by calculating the Pearson product-moment correlation coefficient of their respective residual time series, \(R^X\) and \(R^Y\). This value is given by the following expression:

\[
r_{i}(R^X, R^Y) = \frac{\sum_{i=1}^{n}(R^X_i - \mu^X_i)(R^Y_i - \mu^Y_i)}{\sqrt{\left[\sum_{i=1}^{n}(R^X_i - \mu^X_i)^2\right]\left[\sum_{i=1}^{n}(R^Y_i - \mu^Y_i)^2\right]}}.
\]

where \(R^X_i\) and \(R^Y_i\) are the residual population densities at year \(i\) in fields \(X\) and \(Y\), respectively, and \(\mu^X_i\) and \(\mu^Y_i\) are the sample means of the two time series, so that

\[
\mu^X_i = \frac{1}{n - 1} \sum_{i=2}^{n} R^X_i, \quad \mu^Y_i = \frac{1}{n - 1} \sum_{i=2}^{n} R^Y_i.
\]

It is not immediately clear, however, what constitutes a statistically significant correlation coefficient. Because we work with time series of finite length and the data are affected by stochastic factors, any given value of the correlation coefficient (eq. [5]) may appear by chance. One must therefore distinguish between the cases in which high absolute values of \(r_i(R^X, R^Y)\) are superficial and the cases in which these values are the result of actual synchronization. To do so, the population data were subjected to a careful statistical analysis; full details of the analysis are given in the appendix, available online.

Assessing the Effects of Time Delay

The correlation coefficient (eq. [5]) is not capable of fully explaining all possible relationships between two field populations. For example, if the fields are coupled by dispersal, then the corresponding biological mechanisms may be subject to time delay. The population census during the survey was done in winter, before the species enters its mobile (flying) stage. Therefore, the effect of dispersal coupling, if any, will only be seen in the next year’s census.

Obviously, the effects of delay are not taken into account by the standard correlation coefficient \(r_i\). To identify such relationships (for a single generational delay of 1 year), we introduce a delay-based correlation coefficient that is calculated between two time series, \(A\) and \(B\), as follows:

\[
r_i(A, B) = \frac{\sum_{i=1}^{n-1}(A_i - \mu_{A,i})(B_{i+1} - \mu_{B,i})}{\sqrt{\left[\sum_{i=1}^{n-1}(A_i - \mu_{A,i})^2\right]\left[\sum_{i=1}^{n-1}(B_i - \mu_{B,i})^2\right]}},
\]

where \(\mu_{A,i}\) and \(\mu_{B,i}\) are defined as follows:

<table>
<thead>
<tr>
<th>Number</th>
<th>Grid reference</th>
<th>Min</th>
<th>Max</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>NY 416779</td>
<td>0</td>
<td>16</td>
<td>4.33</td>
</tr>
<tr>
<td>2</td>
<td>NS 114668</td>
<td>2</td>
<td>41</td>
<td>12.33</td>
</tr>
<tr>
<td>3</td>
<td>NX 716619</td>
<td>0</td>
<td>13</td>
<td>3.67</td>
</tr>
<tr>
<td>4</td>
<td>NX 724573</td>
<td>0</td>
<td>15</td>
<td>3.93</td>
</tr>
<tr>
<td>5</td>
<td>NY 049748</td>
<td>0</td>
<td>22</td>
<td>4.73</td>
</tr>
<tr>
<td>6</td>
<td>NX 071353</td>
<td>2</td>
<td>23</td>
<td>6.93</td>
</tr>
<tr>
<td>7</td>
<td>NX 057356</td>
<td>1</td>
<td>24</td>
<td>6.53</td>
</tr>
<tr>
<td>8</td>
<td>NY 101852</td>
<td>0</td>
<td>11</td>
<td>2.20</td>
</tr>
<tr>
<td>9</td>
<td>NS 639691</td>
<td>0</td>
<td>23</td>
<td>4.13</td>
</tr>
<tr>
<td>10</td>
<td>NS 402392</td>
<td>0</td>
<td>13</td>
<td>3.53</td>
</tr>
<tr>
<td>11</td>
<td>NY 278435</td>
<td>1</td>
<td>20</td>
<td>8.07</td>
</tr>
<tr>
<td>12</td>
<td>NR 698229</td>
<td>0</td>
<td>12</td>
<td>4.33</td>
</tr>
<tr>
<td>13</td>
<td>NX 008680</td>
<td>0</td>
<td>33</td>
<td>5.53</td>
</tr>
<tr>
<td>14</td>
<td>NS 452152</td>
<td>2</td>
<td>15</td>
<td>7.73</td>
</tr>
<tr>
<td>15</td>
<td>NX 093520</td>
<td>0</td>
<td>8</td>
<td>4.07</td>
</tr>
<tr>
<td>16</td>
<td>NX 463378</td>
<td>0</td>
<td>24</td>
<td>9.47</td>
</tr>
<tr>
<td>17</td>
<td>NS 412331</td>
<td>0</td>
<td>27</td>
<td>6.60</td>
</tr>
<tr>
<td>18</td>
<td>NX 377452</td>
<td>0</td>
<td>11</td>
<td>4.53</td>
</tr>
<tr>
<td>19</td>
<td>NS 046674</td>
<td>1</td>
<td>24</td>
<td>8.87</td>
</tr>
<tr>
<td>20</td>
<td>NY 693537</td>
<td>0</td>
<td>16</td>
<td>4.07</td>
</tr>
<tr>
<td>21</td>
<td>NY 426783</td>
<td>0</td>
<td>16</td>
<td>6.80</td>
</tr>
<tr>
<td>22</td>
<td>NY 394758</td>
<td>2</td>
<td>21</td>
<td>7.07</td>
</tr>
<tr>
<td>23</td>
<td>NS 369400</td>
<td>0</td>
<td>25</td>
<td>6.00</td>
</tr>
<tr>
<td>24</td>
<td>NS 659461</td>
<td>1</td>
<td>48</td>
<td>9.53</td>
</tr>
<tr>
<td>25</td>
<td>NR 661199</td>
<td>0</td>
<td>16</td>
<td>5.60</td>
</tr>
<tr>
<td>26</td>
<td>NS 324683</td>
<td>0</td>
<td>20</td>
<td>3.93</td>
</tr>
<tr>
<td>27</td>
<td>NS 265446</td>
<td>0</td>
<td>32</td>
<td>11.53</td>
</tr>
<tr>
<td>28</td>
<td>NS 562727</td>
<td>1</td>
<td>17</td>
<td>6.33</td>
</tr>
<tr>
<td>29</td>
<td>NX 743601</td>
<td>0</td>
<td>17</td>
<td>4.60</td>
</tr>
<tr>
<td>30</td>
<td>NS 839734</td>
<td>0</td>
<td>20</td>
<td>4.47</td>
</tr>
<tr>
<td>31</td>
<td>NS 053638</td>
<td>1</td>
<td>41</td>
<td>12.27</td>
</tr>
<tr>
<td>32</td>
<td>NS 111703</td>
<td>1</td>
<td>32</td>
<td>8.20</td>
</tr>
<tr>
<td>33</td>
<td>NS 385235</td>
<td>1</td>
<td>36</td>
<td>7.93</td>
</tr>
<tr>
<td>34</td>
<td>NS 440289</td>
<td>0</td>
<td>20</td>
<td>6.00</td>
</tr>
<tr>
<td>35</td>
<td>NS 671956</td>
<td>0</td>
<td>34</td>
<td>6.73</td>
</tr>
<tr>
<td>36</td>
<td>NN 943236</td>
<td>0</td>
<td>8</td>
<td>2.33</td>
</tr>
<tr>
<td>37</td>
<td>NS 129682</td>
<td>0</td>
<td>23</td>
<td>5.67</td>
</tr>
<tr>
<td>38</td>
<td>NY 203711</td>
<td>0</td>
<td>24</td>
<td>6.47</td>
</tr>
</tbody>
</table>

Note: Field numbering corresponds to that used in figure 1.

Max, maximum; min, minimum.
Figure 2: Plot of population counts against time for five example fields. Fields were chosen on the basis of geographic position; specifically, four are on the edges of the study area (field 36 at the northern end, field 21 at the eastern end, field 16 at the southern end, and field 25 at the western end), and the fifth is in the center (field 14). Mean count across all 38 fields in the study was determined for each year and is also plotted (black line).

\[
\mu_{A,i} = \frac{1}{n-1} \sum_{i=1}^{n-1} A_i, \quad \mu_{B,i} = \frac{1}{n-1} \sum_{i=2}^{n} B_i. \tag{8}
\]

We emphasize that, generally speaking, \( r_i(A, B) \neq r_i(B, A) \). Therefore, the delay-based correlation coefficient separates the effect that the populations of field \( A \) have on field \( B \) (described by \( r_i(A, B) \)) from the effect that the population of field \( B \) may have on \( A \) (described by \( r_i(B, A) \)). In other words, it takes into account a possible asymmetry in the interfield coupling. Such asymmetry can occur, for instance, when insect dispersal is assisted by the wind in cases in which the wind has a prevailing direction (Gatehouse 1997; Compton 2002). This kind of asymmetry reflects what is essentially a traveling wave, as has been observed in the dynamics of childhood diseases (Rohani et al. 1999).

It remains, then, to determine which time series this coefficient should be calculated for. An immediate analogue of the comparison used in the undelayed case would use \( r_i(R^A, R^B) \). This would then compute the degree to which deviations from internal dynamics of one population affect deviations from the internal dynamics of another population. However, here we argue that this is not a meaningful measurement. Instead, we are interested in how the absolute population in one location (regardless of whether it is higher or lower than internal dynamics would predict) may affect the population dynamics at an-
Other location. The strength of this relationship should then be described by $r(X, R')$, and hence this value will be used below. Note that, in this case, the asymmetry lies not only in the correlation coefficient but in the series that are compared.

Results

The Effect of Distance on Strength of Correlation

Several earlier studies have shown that there exists a clear “synchrony versus distance pattern” in which the correlation between population abundances tends to decrease as the distance between the populations increases (Sutcliffe et al. 1996; Lundberg et al. 2000; Peltonen et al. 2002). A reasonable initial hypothesis, therefore, seems to be that populations in fields that are close together are more likely to exhibit synchronization than populations that are spatially more separated. To investigate this hypothesis, the correlation coefficients obtained for each pair of fields are plotted against the distance between the fields; see figure 5a for $r_0$ (no time delay) and figure 5b for $r_t$ (time delay of 1 year).

A visual inspection, however, does not reveal any clear pattern. We observe that, indeed, some fields are strongly synchronized up to a distance of 150–170 km; this happens both with and without time delay. There are also fields that are significantly anticorrelated. On the other hand, for any interfield distance (including the cases of apparent proximity), there are fields that are not correlated at all. On the whole, the plots for $r_0$ and $r_t$ are broadly similar, although stronger negative correlations are observed for the time-delayed case. We therefore conclude that, as such, the absolute distance between fields cannot be the only controlling factor in whether the populations of two fields synchronize. Hence, more information about the “geometry” of the environment has to be taken into account.

This qualitative understanding can be made more rigorous using linear regression analysis. The results are plotted as solid lines in figure 5. Interestingly, the regression analysis of correlation with respect to distance reveals different behavior between the two cases. In the no-delay case, the correlation strength shows a tendency to decrease as distance increases. The gradient of the slope is small (approximately $-0.0074$) but statistically significant, with a $P$ value below .01. The correlation coefficient predicted by the best-fitting line is approximately 0.2 at small distances, and it approaches zero for distances on the order of 300 km. In the time-delayed case, the correlation strength is not significantly different from 0 for any distance range.

The existence of the interfield coupling over the whole area becomes even more evident if the correlation-versus-distance analysis is restricted to statistically significant values only. The results are shown in figure 5c, 5d. In the no-delay case all the significant correlation coefficients appear to be positive and have a relatively large value between 0.5 and 1.0 (fig. 5c). In the time-delay case, all the statistically significant correlation coefficients are large and negative (fig. 5d). Surprisingly, in neither of the two cases does the correlation strength show any decay with distance; on the contrary, the two best-fitting lines have gradients.

1 Note that the time-delayed case includes twice as many points as the no-delay case.
The Effect of Direction on Sign of Correlation

In the previous section, we showed that the population dynamics of *Tipula paludosa* in the study area are synchronized over large distances, although the interfield distance alone provides a rather poor description of the synchronization pattern, especially in the time-delayed case (fig. 5b). More details of the synchronization pattern can be obtained if we consider the relative positions of fields whose populations are correlated. This can be described in part by the directions of the lines connecting any pair of fields (i.e., by considering the bearing of one field from another).

A quantitative insight into how relationships between populations vary with respect to bearing can be made by considering the relative frequency of positive and negative correlation values in a given bearing range. That is, given a bearing range (e.g., $0^\circ$–$10^\circ$), we divide the number of
positive (or equivalently negative) correlation values obtained in that range by the total number of correlation values obtained in that range. The resulting histograms for correlations computed with and without a time delay are shown on a unit circle in figure 6. Note that, to take into account the different tendency observed in the delayed and nondelayed cases (as seen from fig. 5a and 5b), for $r_0$, we present the fraction of positive correlations obtained, whereas for $r_1$, we present the fraction of negative correlations obtained.

It is readily seen that, when no time delay is considered, the relative frequency of positive and negative correlations is approximately independent of bearing, and positive relationships (shown by the thick solid line in fig. 6a) are clearly more common over the whole circle. In contrast, when a time delay is introduced, the relative frequency of positive and negative correlations is strongly dependent on the bearing between the fields. Negative correlations (shown by the thick solid line in fig. 6b) prevail in the range of bearings between southeast and due north, whereas in the remainder of the range, positive correlations dominate. We therefore conclude that the synchronization pattern has a clear directional aspect.

**Analysis of Wind Pattern**

Weather conditions are known to have a significant impact on the population dynamics of many insect species (Baars and Van Dijk 1984; Williams and Liebhold 1995; Raimondo et al. 2004). In particular, the direction and strength of the wind have been proven to be factors strongly affecting the dispersal of flying insects (Gatehouse 1997; Compton 2002). Aiming to explain the observed directional asymmetry in the synchronization pattern, we therefore now turn our attention to the weather pattern. Indeed, synchronization between local populations is known to result from either the Moran effect or dispersal coupling between habitats. It seems improbable that the regional stochasticity (e.g., short-term stochastic variation in the local temperature and humidity) could possess a directional aspect. In contrast, the existence of a prevailing wind direction, if any, obviously can make the coupling asymmetric.

Measurements of wind velocity were recorded at four weather stations spanning the study area (Dundrennan, Abbottsinch, West Freugh, and Tiree; fig. 1). The time series are obtained from a single year, 1987, which we assume to be representative for the whole duration of the survey. The data cover a 2-month period, August to September. This period corresponds to peak adult emergence of *T. paludosa* and thus is the time in which interactions between dispersed populations are most likely. The data

![Figure 6](image-url)
comprised hourly measurements of the average wind speed and the wind direction (Met Office 2011).

Distributions of average wind speed are shown in figure 7a–7d. The weather stations at West Freugh and Tiree tend to report higher wind speeds than the less exposed stations at Dundrennan and Abbotsinch, presumably because higher wind speeds can be sustained over the relatively flat surfaces of the surrounding seas and wide stretches of water. In contrast, the wind direction appears to be less influenced by local terrain, as is shown by the comparison between figure 7e–7h and figure 1. The stations at West Freugh, Abbotsinch, and Dundrennan suggest that winds predominantly blow either due south or between the southeast and the north; at Tiree, the separation between these two modes is less pronounced. In general, there is very little wind blowing in the south to northwest sector. This is in strikingly good agreement with the pattern shown in figure 6b.

Spatial Cross-Correlations with No Time Delay

In “The Effect of Distance on Strength of Correlation” and “The Effect of Direction on Sign of Correlation,” we quantified the cross-correlations between fields by pooling all correlations together. In particular, the existence of correlations between the local populations (with no time delay) across the region “on average” was shown by finding the best-fitting line to the whole array of pairwise correlation coefficients versus distance (fig. 5). The existence of a directional aspect (to the time-delayed relationships) was revealed by plotting a histogram of (weighted) correlation coefficients on a circle (i.e., as a function of the bearing; fig. 6). However, these cumulative properties obscure the role of individual fields. Meanwhile, revealing the contribution of individual fields may be important for better understanding the process behind the observed pattern. The contribution from different pairs of fields to the “synchronization versus distance” pattern, as given by figure 5, varies significantly regardless of the distance between them, and hence one might wish to understand why. In addition, the terrain in the study region is highly heterogeneous. It includes hills, valleys, plains, and urban areas as well as some considerable stretches of water (e.g., Firth of Clyde). Different local populations are therefore exposed to quite diverse environments that vary in both terrain and weather conditions.

To analyze the impact of precise positional relationships between fields, we now consider all fields individually. In this section, we consider the correlations calculated without time delay (see eq. [5]). The results are summarized in figure 8. For each given field X, we count the number of the fields where the residual population dynamics of T. paludosa are significantly correlated (at the 5% significance level) to the residual population dynamics in X. Note that, in this case, all the significant correlation coefficients had a positive sign (fig. 5c). The result is shown by the length of a bar based at the location of each field. The shortest bar (with a length of 0.5 units on the map scale) means that one other population is significantly correlated to this population. The largest number of fields significantly correlated to a given one is found to be 10 (with the length of the corresponding bar thus being set to 5 units on the map scale). For the three fields that do not have a significant correlation to any other field in the array, the bar has length 0, and so their position is shown by a dot.

It is readily seen that the map shows a clear divide between parts of the region above and below the dashed line (which has been included for ease of comparison). In the northeast region, above the dashed line, most of the populations are correlated with a large number of other populations (4.27 on average). In contrast, in the southwest region, below the dashed line, populations are correlated to significantly fewer populations (1.75 on average).

The information shown in figure 8 is, however, incomplete until the position of the mutually correlated fields is known. Consider a hypothetical case that field X is significantly correlated to fields A, B, and C; one then might wish to know where fields A, B, and C are situated with respect to X. Figure 8 is therefore complemented with figure 9. In figure 9a, the arrows (now normalized to a unit length) indicate the average direction to all fields (e.g., A, B, and C) whose populations are significantly correlated to that in the given one (e.g., X). If a given field is correlated to just one other field, then the corresponding arrows point toward each other. In figure 9b, any significant relationship between two populations is indicated by a dotted line. Figure 9a can be considered a summary of the relationships between a field and the remaining populations, whereas figure 9b provides an overview of the networks of relationships formed between these populations. Because the weather conditions are expected to be important, to give a visual idea about the impact of the wind velocity, the position of each weather station is indicated by the intersection of two dashed lines. The solid lines originating from this intersection replicate the histograms of wind direction given in figure 7.

---

2 Original data were supplied by the Met Office, which provided hourly data on relative humidity, precipitation, cloud cover, sunshine amount, and wind speed for Abbotsinch and Tiree for the period August 1 to September 30, 1987; hourly data on relative humidity and wind speed for West Freugh and Dundrennan for the period August 1 to September 30, 1987; and 30-year monthly average data (relative humidity, wind speed, and hours of sunshine) for the counties of southwest Scotland, based on observations made between 1971 and 2000. See also http://www.metoffice.gov.uk.
Figure 7: Histograms of average wind speed (a–d) and wind direction (e–h) over the study period at four weather stations. Wind direction histograms are in polar form and are laid out in the same order as those of average wind speed.
apart from a few exceptions, the strongly correlated fields in the northeast region appear to be mostly correlated between themselves and form a dense network that largely excludes fields in the southwest. The fields in the southwest region form a similar, if sparser, network, with limited interconnections with the northeast network. This provides additional evidence for the existence of a division between the northeast and southwest regions.

The results shown in figure 9 confirm that geographical proximity does not appear to be a factor controlling what fields are correlated. It is readily seen that there are many situations in which a field is not correlated to its immediate neighbor(s) but is significantly correlated to fields much farther away.

**Spatial Cross-Correlations with a Time Delay**

In the previous sections, we have shown that the standard correlation coefficient (eq. [5]) is not able to describe all possible relationships between two fields (figs. 5 and 6). A dispersal mechanism is likely to be detected only when a time delay is introduced between two populations. An analysis of the relationships between influencing populations and influenced residual populations with a generational delay (of a single year in this case) can be performed in a similar way to that presented in the last section. Again we limit our attention to those relationships that are significant at the 5% level. The plots below (figs. 10 and 11) are therefore analogous in concept to figures 8 and 9.

As we previously observed, the time delay introduced in equation (7) breaks the symmetry implicit in the standard correlation coefficient (eq. [5]). Consequently, it is
possible to consider two classes of relationships between a given population and the other populations. The first class is the set of residual populations that, when delayed by 1 year, are correlated to a given population (i.e., the set of populations influenced by a given population). The second class is the set of populations that are correlated to a given residual population when it is delayed by 1 year (i.e., the set of populations influencing a given population).

In figure 10, the number of populations influenced by and influencing a given field population is shown by the length of a bar above and below the field position (indicated by a plus sign), respectively. The scale of these bars is as described in the previous section. Note that, in contrast to the relationships presented in the previous section, all of the statistically significant time-lagged relationships now have negative coefficients (figure 5d).

As in the previous section, we add reference lines to divide the study area into three regions, referred to as southwest, central, and northeast. The average number of fields influenced by a population in any given region is (approximately) constant across the three regions, with values of 1.38, 1.94, and 1.54 in the southwest, central, and northeast regions, respectively. In contrast, the average number of populations influencing a given population varies significantly across these regions, taking values of 0.125,
1.12, and 3.38 in the southwest, central, and northeast regions, respectively. Thus, populations in the southwest are more likely to influence other populations than to be influenced themselves, whereas populations in the northeast show the opposite trend. Populations in the central region influence other populations and are influenced themselves at roughly equal levels.

As in the previous section, we complement these data with plots that show the directions between fields and the populations that they influence or are influenced by (figure 11). In figure 11a, red arrows indicate the average direction to residual populations that a given population significantly influences. Blue arrows indicate the average direction to populations that significantly influence a given residual population. In figure 11b, all significant relationships are represented by a two-color line connecting the fields between which the relationship exists. The red section of this line connects to the influencing field, whereas the blue section of the line connects to the influenced field.

Including the positional information in our analysis of this pattern again produces additional understanding. The strong correlations within regional groupings observed in the undelayed case are, for the most part, absent. Instead, southwest populations appear to influence central populations, which, in turn, influence northeast populations in an apparent cascade; see, for example, the relationships between fields along the southern edge of the study area. Similar interactions can be seen between the populations of the northern corner and those to their southeast, although the interaction is less pronounced.

The distribution of bearings from significantly influencing to influenced is presented as a histogram in figure 12. It is clear that this distribution deviates noticeably from the underlying distribution of bearings between fields in the study area (shown by the gray line in fig. 12); therefore, the observed directional asymmetry cannot be reduced to the effect of the system geometry. The most significant deviations from this underlying distribution lie between the southeast and the north. Because all of these relationships have negative correlation coefficients, this is in good agreement with the trend observed in figure 6. Furthermore, it corresponds well to the pattern shown in figure 11.

Discussion and Conclusions

In this article, we have considered the population dynamics of an insect pest, *Tipula paludosa*, on a habitat consisting of 38 agricultural fields in southwestern Scotland. The annual data on population abundance collected in a survey accomplished during 1980–1994 were analyzed. Our goal is threefold. First, we want to reveal whether there is a correlation between the fluctuations in local populations, the phenomenon known as synchronization (Lundberg et al. 2000; Liebhold et al. 2004). Second, we want to reveal the corresponding spatial pattern (i.e., how the degree of synchronization between fields changes in space and, in particular, with interfield distance). Third, we want to understand the process(es) resulting in the observed synchronization pattern (i.e., to relate the observed properties of the *T. paludosa* metapopulation to a specific mechanism or factor).

The first goal is relatively simple to reach. We have calculated all cross-correlation coefficients as given by $r_0$ (see eq. [5]) and found that only a small fraction of fields are uncorrelated or weakly correlated (e.g., $|r_0| < 0.1$). A majority of population pairs are positively correlated, and in many cases, $r_0$ is as large as 0.5 or even higher (fig. 5a). There are also a considerable number of pairs that are negatively correlated, with typical values of $r_0$ between $-0.1$ and $-0.3$.

With regard to the spatial pattern, whether synchronization is due to dispersal or the Moran effect, it is reasonable to suppose that the cross-correlation coefficient should decrease with the distance (Liebhold et al. 2004). We have shown, however, that this expectation is rather oversimplified. Although the best-fitting line obtained by using the linear regression analysis indeed has a negative slope (fig. 5a), a closer look at the correlation strength versus distance immediately reveals that this “prediction”
about the decay in synchronization is rather superficial. Instead, synchronization exhibits an intermittent behavior. For any range of the interfield distances, from very small (a few kilometers) to very large (up to 200 km), there are fields that can be strongly positively correlated, negatively correlated, or virtually uncorrelated. In case the analysis is restricted to the statistically significant correlations only (fig. 5c), the decrease in the correlation strength with distance is not seen at all, at least up to the scale of 200 km.

In addition to the usual cross-correlation coefficient \( r_0 \), we also calculated a delay-based cross-correlation coefficient \( r_1 \) as given by equation (7). Such a delay (assumed to be 1 year, which is the equivalent of one generation for \( T. paludosa \)) can arise if synchronization is induced by dispersal. Recall that the population data were collected in midwinter, when the species is in its larval stage. Dispersal is, however, associated with the flying stage that normally happens in late August and early September. Therefore, the effect of dispersal will not be seen in the census until the next year. The effect of delay is likely to be felt more strongly if dispersal is asymmetric (e.g., if field \( X \) delegates a fraction of its population to field \( Y \) but not vice versa). In contrast, synchronization due to the impact of stochasticity is unlikely to be subject to delay.

Interestingly, \( r_1 \) exhibits properties significantly different from \( r_0 \) (fig. 5). The values of \( r_1 \) are predominantly negative, especially if the analysis is restricted to statistically significant values (fig. 5d). There is no decay with distance at all, because the best-fitting line has a slope very close to zero. Contrary to \( r_0 \), the time-delayed coefficient \( r_1 \) shows a clear directional aspect (fig. 6) so that the relationship between fields appears to be stronger in the east-northeast and southeast directions than on other bearings (fig. 12). This is in good agreement with meteorological data on wind direction; thus, we suggest that dispersal is wind assisted. Note that we are not able to provide a more quantitative proof of the impact of the wind on population synchronization (e.g., by calculating a correlation coefficient between the bearing of the pairwise correlations and the wind velocity). Such calculation would require high-resolution data on the wind direction across the whole study area; unfortunately, such data do not exist.

Note that, from the whole range of environmental factors, we only explicitly consider wind, thus regarding other factors as environmental stochasticity. Another relevant factor can be precipitation. However, rainfall has a significant impact on the population abundance only when autumn is exceptionally dry (Milne et al. 1965; Blackshaw and Petrovskii 2007), and there is no evidence of any abnormal precipitation level in southwestern Scotland during the period of study.

In this study, we have investigated the synchronization pattern obtained for a time lag of 1 year. This choice seems to be suggested by \( T. paludosa \) life traits. However, we have also considered longer time delays of 2 and 3 years. The corresponding cross-correlation coefficients \( r_2 \) and \( r_3 \) show properties similar to those of \( r_1 \); in particular, the networks of interfield connections (not shown here for the sake of brevity) have shapes that are only slightly different from those shown in figure 11, with a few links having disappeared and a few new links having emerged. A general tendency seen with an increase in time lag is a gradual decrease in the average correlation strength. The essential features of the time-lagged correlations are therefore encompassed by the coefficient \( r_0 \).

The differences between \( r_0 \) and \( r_1 \) can be used to distinguish between the contribution from dispersal and the Moran effect, which is the third goal of our study. We associate the no-delay coefficient \( r_0 \) with the effect of environmental stochasticity and associate the delay-based coefficient \( r_1 \) with dispersal. Because synchronization is seen both with and without time delay, we conclude that both mechanisms are involved.

A counterintuitive finding is that both mechanisms operate on the same spatial scale of approximately 200 km, as given by the size of the study area. With regard to dispersal coupling, it seems to be a surprising result, because \( T. paludosa \) females are known to be poor flyers with typical dispersal distances that are thought to be less than 100 m. For species with poor dispersal abilities, synchronization attributable to dispersal is thought to occur on a spatial scale much smaller than that of synchronization attributable to the Moran effect (Sutcliffe et al. 1996; Peltonen et al. 2002). However, this obviously does not account for the potential impact of wind, which would not only provide a directional effect but also uncouple any dispersal-distance relationship at smaller scales. What can be true for forest insects may not necessarily be true for insects dwelling on the bare plains and hills of southwestern Scotland. With a wind speed of several meters per second (which is typical for the study area; fig. 7), the air flow is strongly turbulent. Turbulence creates ascending currents that can keep individual insects in the air for many hours (also taking into account the complicated body shape and the relatively large wingspan of the crane fly), which is sufficient time for them to reach another breeding ground situated a long distance away from their natal field.3 We note that, although direct evidence of wind-assisted dispersal for \( T. paludosa \) is not available, “sailing with the wind” is a typical dispersal strategy for many other insect species, with distances covered being dozens and even hundreds of kilometers (Gatehouse 1997; Compton

3 Tipula paludosa have been caught in suction traps at 14 m above ground in samples collected as part of the Rothamsted Insect Survey (R. Blackshaw, unpublished data).
species that exerts a consistent, regulatory effect on
(Liebhold et al. 2004). However, we are not aware of any
interaction with another species that is itself synchronized
(Liebhold et al. 2004). However, we are not aware of any
species that exerts a consistent, regulatory effect on
T. paludosa populations, and so we consider this possibility
the least likely explanation. Second, because T. paludosa
is a pest, its abundance is controlled by pesticides. Should
the application of pesticides be synchronized across the
region, it could possibly synchronize the dynamics of the
pest. However, the existing agricultural legislation in the
United Kingdom does not impose on farmers any oblig-
atory response to pest infestation. Not only are pest-con-
trolling measures purely voluntary, but so too is partici-
pation in monitoring programs. The probability of a
synchronized application of pesticides is therefore unlikely.
Any regular or synchronized pesticide treatment of the
fields used in our study is not documented. Note that,
even in a general case of pest monitoring in which a syn-
chronized application of pesticides cannot be ruled out, it
can hardly explain the directional patterns in synchrony.

Additional evidence of the coupling by the wind-assisted
dispersal may also be obtained by developing a more de-
tailed theoretical framework that operates across the whole
range of spatial scales involved. Indeed, a comprehensive
model of the dynamics of an individual population must
take all of the local populations into account. Correspon-
dingly, it should take into account environmental processes
that act on a regional scale along with those that act on a
local scale. In particular, such a model should make use of
the patterns in directionality observed (fig. 12) to estimate
the probability that a given population will be influenced
by any other population in the study area. A functional
relationship describing the effect of one population on an-
other could then be derived in a similar way to that used
to obtain equation (1) but weighted with the probabilities
of given interactions with respect to distance and bearing.
In conjunction with equation (1), this would provide a more
complete description of a given population’s region-wide
dynamics. However, parameterization and verification of
such a model can hardly be possible until the impact of
wind and terrain are incorporated explicitly into these func-
tional relationships. This is a complex task that clearly lies
beyond the scope of this article; in particular, more detailed
weather data would be required.

Given the evidence presented, the dynamics of appar-
etly isolated populations of T. paludosa cannot be com-
pletely described by internal mechanisms (e.g., by density
dependence). Instead, these dynamics are noticeably in-
fluenced by the dynamics of populations of this species at
other locations. Results of our analysis indicate that the
wind is likely to be a factor responsible for the interhabitat
coupling on the spatial scale up to 200 km. This is rather
counterintuitive, because T. paludosa are usually regarded
as poor fliers. A study to look for genetic similarities be-
tween different populations across the whole area could
confirm the existence of interhabitat coupling by direct
transport. We are considering undertaking such an inves-
tigation in the future.

Although we have focused on the dynamics of a par-
ticular species in this article, we believe that our approach
and findings may be useful in a much broader context.
Synchronization of population fluctuations often occurs
as a result of a combination of the effects of environmental
stochasticity and dispersal. Discriminating between these
two mechanisms is a considerable challenge, especially
where they act on the same spatial scale. By studying the
coupling between local populations with a time lag of one
generation, we demonstrate a general method for sepa-
rating the mechanisms. Indeed, it is hard to see how spa-
tially correlated stochastic fluctuations in weather condi-
tions (as required by the Moran theorem) can possibly
deliver a time-lagged coupling. The general message, there-
fore, is that within-generation synchrony can be attributed
to the environment, whereas synchrony with a shift be-
tween generations (i.e., time lagged) is due to dispersal.

Acknowledgments

We thank D. McCracken of Scotland’s Rural College for
providing the original data. The work was partially sup-
ported by the Leverhulme Trust through grant F/00 568/X.

Literature Cited

carabid beetles at a Dutch heathland. I. Subpopulation fluctuations
in relation to weather and dispersal. Journal of Animal Ecology
53:375–388.
Blackshaw, R. P. 1983. The annual leatherjacket survey in Northern
Ireland, 1965–1982, and some factors affecting populations. Plant
Pathology 32:345–349.
Blackshaw, R. P., and C. Coll. 1999. Economically important leather-
jackets of grassland and cereal: biology, impact and control.
of leatherjackets (Tipula paludosa Meig). Journal of Applied
Blackshaw, R. P., and S. V. Petrovskii. 2007. Limitation and regulation


Associate Editor: Andrew R. Solow
Editor: Troy Day