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Self-organization and pattern formation represent the emergence of order in temporal and spatial processes. Self-organization in population ecology is gaining attention due to the recent advances concerning temporal fluctuations in the population size of dispersal-linked subunits. We shall report that spatially structured models of population renewal promote the emergence of a complex power law order in spatial population dynamics. We analyse a variety of population models showing that self-organization can be identified as a temporal match in population dynamics among local units, and how the synchrony changes in time. Our theoretical results are concordant with analyses of population data on the Canada lynx.

Keywords: self-organization; spatial population dynamics; autoregressive processes; synchrony; power spectrum; Canada lynx

1. INTRODUCTION

The study of the evolution of order in spatial and temporal processes, i.e. self-organization (Kauffman 1993), aims at finding general laws for characterizing the nature of these processes in different fields of science (Fagerström *et al.* 1996; Anonymous 1999). In population ecology, where the general rules are exemplified by models of population dynamics (Lotka 1925; Beverton & Holt 1957; May 1981; Royama 1992), the topic has recently attracted increasing interest due to the rapid development of spatial ecology (Bascompte & Solé 1997; Tilman & Kareiva 1997). So far, self-organization has been detected by eye in model simulations because of the attractive patterns generated (Hassell *et al.* 1991, 1994; Solé & Valls 1991; Comins *et al.* 1992; Solé *et al.* 1992; Ranta & Kaitala 1997; Kaitala & Ranta 1998). That populations may have a temporally organized structure is suggested by the self-repeating cyclic dynamics of Canada lynx and snowshoe hare populations (Elton & Nicholson 1942), by various grouse species and by Scandinavian voles and lemmings (Lindén 1981; Lindström *et al.* 1996, 2001). It is common for these cycle-prone species that, within a taxa, populations tend to fluctuate in step over large geographical areas (Elton 1924; Elton & Nicholson 1942; Lindström *et al.* 2001), also indicating, at least to some degree, the potentiality of spatial organization in their dynamics.

Here we report that, in a spatial setting of semi-independent subunits connected via dispersing individuals, ecological models of population renewal are capable of supporting the evolution of complex order in their dynamics. In particular, we identify self-organization at the level of synchronicity in local dynamics in a spatially explicit context for a variety of population dynamics types. Instead of looking at visually identifiable (and often attractive) spatial patterns, we shall characterize the emerging patterns quantitatively. We focus on the temporal and spatial patterns of synchrony in the dynamics at different locations of the dispersal-linked population subunits. We show that the model-generated dynamics become self-organized such that the synchrony measures between population fluctuations in the subunits and their dependence on the interunit distance show a power law structure. In other words, self-organization becomes quantitatively identifiable at the level of temporal synchronicity in the subunit dynamics such that the synchrony, when measured using a time-windowing technique (Ranta *et al.* 1997*a*), shows temporally scale-free, self-similar dynamics in time.

2. SEARCHING ORDER IN SPATIAL POPULATION DYNAMICS

In our model, the space is composed of dispersal-coupled population subunits, each of which is governed by a local population renewal process. The spatial structure consists of *n* randomly distributed units in a two-dimensional coordinate space. In order to obtain a general view of the patterns emerging, we assume that, at the local level, the population dynamics are governed either by a Moran–Ricker model with delayed density dependence (Turchin 1990; Royama 1992) or by linear autoregressive models (Box & Jenkins 1976) of orders 1 or 2, i.e. AR(1) or AR(2). The population subunits are coupled by distance-dependent dispersal such that, in each time-step, a given fraction of newborn individuals leave their place of birth in order to reproduce elsewhere. The temporal dynamics in each patch are affected by local noise and global Moran noise (e.g. Ranta *et al.* 1995).

The spatial population dynamics were generated by simulations. Delayed density dependence in the Moran–Ricker model (Turchin 1990; Ranta *et al.* 1997*a*, 1999) with proper parameter selection allows us to generate cyclic population dynamics with approximately four-, six- and ten-year period lengths. The temporal match in

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synchrony in pairs between the 25 population subunits was scored by using a time-lag zero cross-correlation, r_0 (Box & Jenkins 1976). We scored the difference between the upper and lower quartiles, i.e. $Q_{3,k} - Q_{1,k}$ at time k, for the 300 pairwise correlation coefficients. The upper (lower) quartiles are indicated by the boundaries of the 25% highest (lowest) scores of synchrony. The simulated time-span was explored with a moving time-window (Ranta *et al.* 1997*a*) in order to score temporal changes in the overall degree of synchronicity. Using this technique we also scored the temporal changes between synchrony and its levelling off with distance, r_D (e.g. Ranta *et al.* 1995, 1999).

(a) *Spatial population dynamics model*

In our model, a total of 25 populations are randomly placed on a 20×20 grid. The local dynamics of the populations are affected by dispersal and local and global noise. Assuming that a fraction m of the population disperses annually, the local dynamics in patch i are given as

$$X_i(k+1) = $$
$$(1-m)F[X_i(k), X_i(k-1), \mu(k), u_i(k)] + \sum_{s, s \neq i} M_{si}(k), \qquad (1)$$

where $X_i(k)$ is the population size in patch i at time k, $\mu(k)$ is the Moran effect, $u_i(k)$ is the local noise and $M_{si}(k)$ is the number of dispersing immigrants arriving at patch i from patch s. The Moran effect is characterized by its annual probability of occurrence $p(k)$ and its intensity μ. We write

$$\mu(k) = \begin{cases} \mu & \text{if } \overline{p} \leqslant p(k) \leqslant 1, \\ 1 & \text{otherwise} \end{cases} \qquad (2)$$

where $0 \leqslant \overline{p} \leqslant 1$ (here $p = 5$). When the noise occurred μ was drawn from uniform random numbers between 0.5 and 1.5.

The number of offspring alive after reproduction in equation (1) is given as

$$F = X_i(k) \mu(k) u_i(k) f[X_i(k), X_i(k-1)], \qquad (3)$$

where the arguments of F have been omitted. Local noise $u_i(k)$ is a random number drawn from a uniform distribution between 0.95 and 1.05. Function f defines the density-dependent per capita reproductive rate.

The populations were left to renew after two differing model categories: the Moran–Ricker dynamics (Turchin 1990) and the linear autoregressive dynamics of orders 1 and 2, AR(1) and AR(2). For the delayed nonlinear Ricker dynamics we write

$$f[X_i(k), X_i(k-1)] = \exp[r(1 - a_1 X_i(k) - a_2 X_i(k-1)], \qquad (4)$$

where r is the maximum per capita rate of increase and a_1 and a_2 are parameters determining density dependence. The autoregressive renewal is given as

$$X_i(k+1) = \phi_1 X_i(k) + \phi_2 X_i(k-1) + \delta + \varepsilon(k), \qquad (5)$$

where ϕ_1 and ϕ_2 are the parameters, δ is a constant (here 2) and ε is a normal random deviate (with mean 0 and variance 0.2). With $\phi_2 = 0$ and $-1 < \phi_1 < 1$ we have the

AR(1) process, whereas in order to achieve AR(2) the following inequalities should be satisfied simultaneously (Box & Jenkins 1976): $\phi_2 + \phi_1 < 1$, $\phi_2 - \phi_1 < 1$ and $-1 < \phi_2 < 1$.

Each year, a proportion m (here $m = 0.05$) of individuals from each patch disperse to neighbouring patches. In equation (1), the number of immigrants arriving at the subpopulation i from the population s is given as

$$M_{si}(k) = \frac{mF \exp(-cd_{si})}{\sum_{j, j \neq s} \exp(-cd_{si})}, \qquad (6)$$

where d_{si} is the distance from s to i and c (here $c = 0.75$) is a constant parameter.

(b) *Simulations*

At the beginning of each simulation the 25 local populations were initiated in random phase. They were then allowed to renew after equations (1) and (4) or (5) for 2^{10} time-steps (in order to remove the transients) and then the next 2^{13} time-steps were used for our analyses. A cross-correlation coefficient with time-lag zero (r_0) was used for characterizing the temporal match in fluctuations between any pair of the population subunits. The time-window used was 2^7 time-steps. Here we are interested in the temporal behaviour of the emerging two new statistics $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$, with k here referring to the kth time-window. Note that the narrower the quartile difference, the higher the overall level of synchrony, which also makes the $r_{D,k}$ values close to zero. Large quartile differences, on the other hand, indicate that there are some populations in tight synchrony while there are also pairs of population subunits fluctuating out of phase or even randomly. This setting allows $r_{D,k}$ to achieve high negative values.

3. RESULTS

The temporal changes in the difference between the quartile boundaries of the synchrony measures show non-cyclic irregular variations over time despite the periodic temporal structure of the population dynamics (figure 1*a*–*c*). So also does the correlation between the pairwise subunit synchrony against the distance between the units. Due to the time-windowing technique, these measures provide us with two time-series for analysis, that is $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$. Interestingly enough, the power spectra of these time-series show a pattern which indicates that the spectra are of the $1/f$ type (Halley 1995).

Our finding (figure 1*i*–*iii*) indicates that the temporal dynamics of a spatially structured population are organized at the level of synchrony among population subunits. In the simulations the long-term average of the synchrony is positive and $r_{D,k}$ is negative suggesting that the population dynamics in the subunits tend to vary in step but in such a way that the synchrony among the subunits decreases with increasing distance. However, the time-windowing technique reveals that the degree of synchrony $Q_{3,k} - Q_{1,k}$ and its relationship against distance $r_{D,k}$ varies over time. Our analysis also shows that the variations in these time-series are by no means entirely random temporal fluctuations. Rather, when analysing
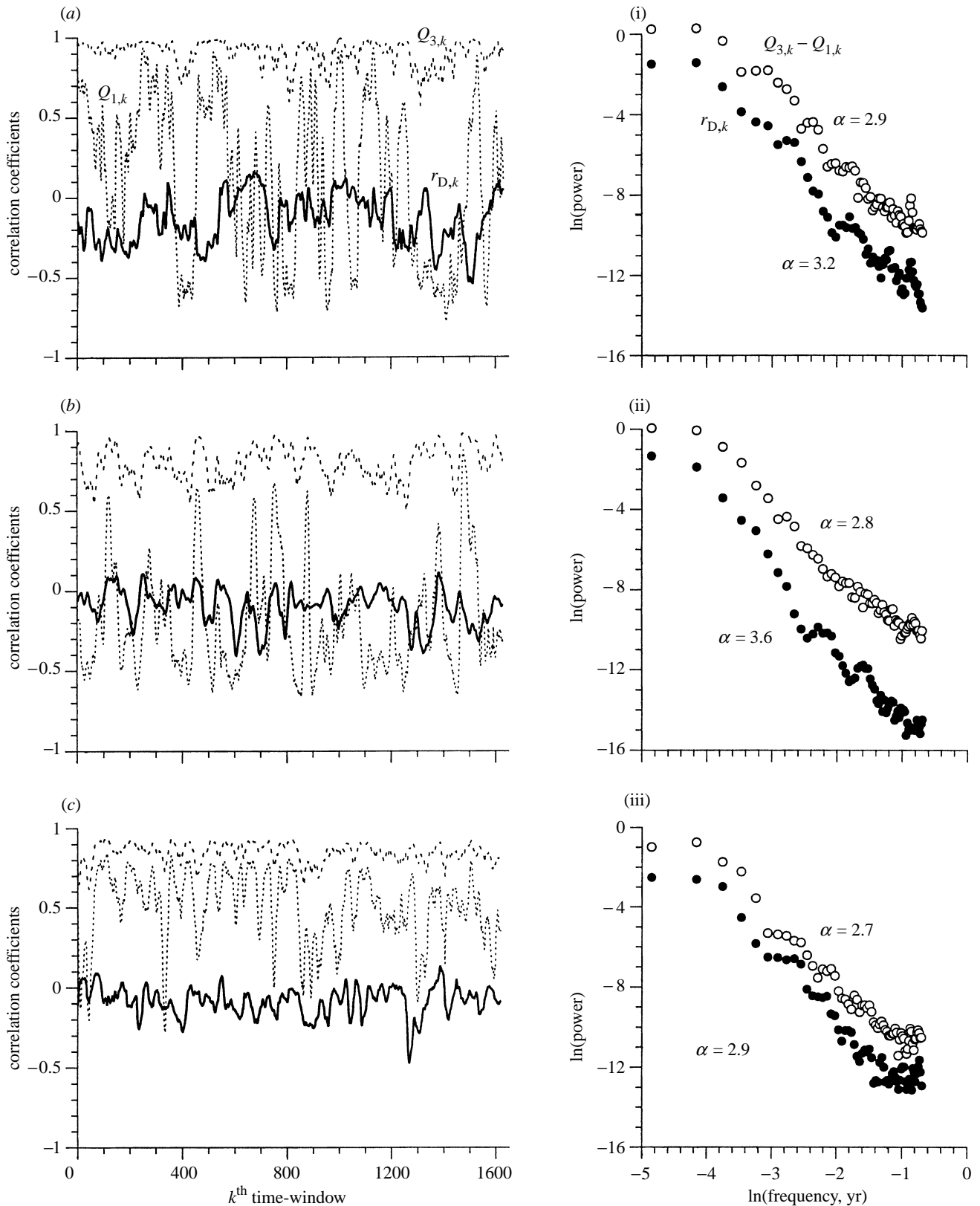
Figure 1. The spatial population dynamics, as simulated using density-dependent population renewal with Moran–Ricker dynamics, become organized at the level of population synchrony. The upper and lower quartiles $Q_{1,k}$ and $Q_{3,k}$ (the two dashed lines) of the synchrony measures vary in time with the local populations obeying period lengths in cyclic dynamics of (*a*) four years, (*b*) six years and (*c*) ten years. The correlation coefficients $r_{D,k}$ describing the relationship between the level of synchrony and the distance between the population subunits compared for the corresponding dynamics are also shown. (i–iii) The corresponding specific power spectra for $Q_{3,k} - Q_{1,k}$ (open circles) and $r_{D,k}$ (filled circles). The linearity of the relationship indicates that they are of the $1/f^{\alpha}$ type, indicating the presence of a power law in the spatial and temporal dynamics (the values of α are inserted).
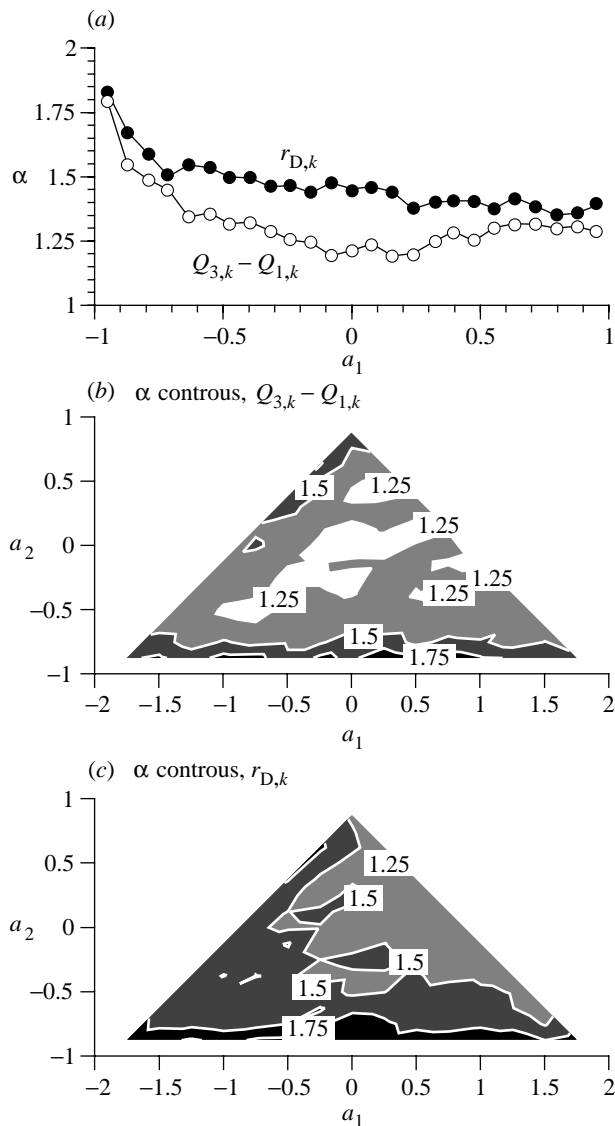
Figure 2. The average values of the slope α of the power spectra of $Q_{3,k} - Q_{1,k}$ (open circles) and $r_{D,k}$ (filled circles) for (a) the AR(1) process and (b,c) AR(2) process. The values in the α contour graphs are averages of ten replicated runs for each parameter value combination possible for the AR(1) and AR(2) processes.
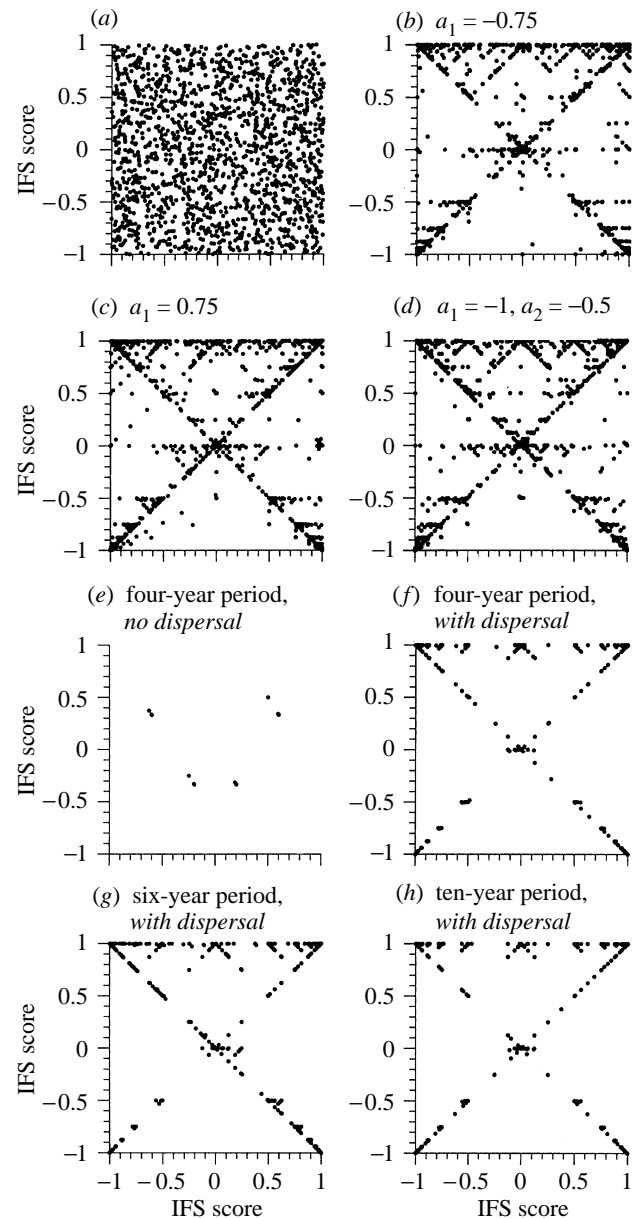

Figure 3. The power law structure of $Q_{3,k} - Q_{1,k}$ analysed with the IFS test graphs for (a) white noise in a non-structured population, (b,c) in two AR(1) processes and (d) in one AR(2) process. (f–h) The IFS scores for spatially structured settings where the local populations obey cyclic dynamics with period lengths of four, six and ten years, respectively. (e) For comparison, the IFS scores for cyclic dynamics with a period length of four years. The temporal structure obeying the power law in the IFS graphs is visible by aggregation of the dots along the diagonals. (The results are the same for $r_{D,k}$, but they are not displayed here due to lack of space).

their dynamics in the frequency domain we observe that the power of the different frequencies obey a power law of the form $1/f^\alpha$, where f is the frequency and α is a constant defining the slope of the power and also the autocorrelation structure of the time-series. The negative slope of the power spectra (positive α) (figure 1i–iii) indicates that long-term fluctuations dominate, thereby giving the time-series positive autocorrelation. More importantly, the linear structure of the power spectra is an indication of the presence of temporal self-similarity in the time-series $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$.

We also verified the property of self-organization using the AR(1) and AR(2) processes (figure 2). Curiously enough, the most red dynamics (the highest values of α) are obtained for the AR(1) processes with parameter values producing negatively autocorrelated population dynamics in the absence of a spatial population structure.

Our results (figure 2) suggest that the autocorrelation structure of the local population dynamics does not determine how the synchronicity among several populations fluctuates with time. In spatial settings both the AR(1) and AR(2) processes yield self-organized dynamics in $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$.

That a positive autocorrelation structure in $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$ (the results are not displayed for $r_{D,k}$) is due to the spatial structure, irrespective of the model generating the local population dynamics, becomes clear from
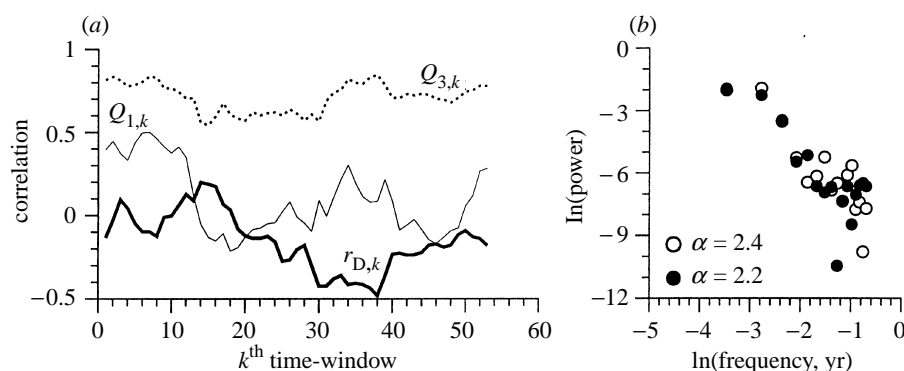
Figure 4. The long-term dynamics of the Canada lynx revisited. The 1919–1985 data are the annual lynx pelt harvest aggregated at the province level. (*a*) Lower $Q_{1,k}$ and upper $Q_{3,k}$ quartiles of the synchrony measures in pairs among the eight Canadian provinces, together with the correlation $r_{D,k}$ between the synchrony level and distance between the provinces compared. (*b*) The corresponding power spectra for $Q_{3,k} - Q_{1,k}$ (open circles) and $r_{D,k}$ (filled circles). The data are analysed by using the time-windowing technique using 15 years as the window length. See also Ranta *et al*. 1997*a*.

comparing the iterated function system (IFS) clumpiness scores (Jeffrey 1992) of the different processes. If the quartile difference in the synchrony $Q_3 - Q_1$ is represented by white noise in a non-structured space the IFS score does not show any pattern (figure 3*a*). However, the spatial structure, with the help of dispersal-linked population subunits superimposed with disturbance, organizes the local dynamics into a spatial dynamics with a self-organized structure. The closer the IFS scores are located around the diagonals the more closely the power spectra are expected to follow the form of $1/f^{\alpha}$. The rich variety of local dynamics explored here all become self-organized (in terms of the temporal synchrony pattern) due to spatial structure only. The structure of points aggregating around the diagonals can be detected for both the AR(1) and AR(2) processes (figure 3*b–d*) and is most clearly pronounced in the cyclic population dynamics irrespective of the period length (figure 3*f–h*). For comparison, we also show the IFS score of the population dynamics with a four-year period in the absence of dispersal (figure 3*e*). Clearly, this pattern, which is also typical for the other cyclic dynamics in the absence of dispersal, does not show any sign of self-organization.

4. DISCUSSION

The occurrence of synchrony between population dynamics in different geographical locations has been verified for a large number of species from different taxa (Hanski & Woiwod 1993; Ranta *et al*. 1995, 1997*b*; Lambin *et al*. 1998; Bjørnstad *et al*. 1999*a,b*; Paradis *et al*. 1999). The dependence of the synchrony level on the geographical distance between locations is also well established (Ranta *et al*. 1999). Note however that all populations examined do not display synchronicity or its levelling off with distance (e.g. Cattadori *et al*. 1999). On the other hand, synchronization of populations may also occur in isolation without dispersal (Moran 1953; Ranta *et al*. 1995), as has been reported for feral sheep populations on two distinct islands (Grenfell *et al*. 1998).

When we analysed the Canada lynx data from eight provinces earlier using the time-windowing technique (Ranta *et al*. 1997*a*), we could show that the synchrony level between any pair of provinces displayed a temporal

structure such that the synchrony can be observed, but that it may well disappear for apparently unpredictable periods. The same data are now examined in more detail by also calculating the new time-series $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$ for the lynx data with the time-windowing technique. Admittedly, the resulting time-series (figure 4) are much shorter than used in the previous simulation analyses. However, the $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$ statistics extracted from the real data (figure 4*a*) resemble those derived from the simulations. We found that, by subjecting the $Q_{3,k} - Q_{1,k}$ and $r_{D,k}$ observations to the power spectra analysis, they could also be described satisfactorily by the $1/f$ power law, with the slopes α (figure 4*b*) well within the range of the values found in our simulations (figures 1 and 2). Thus, it is tempting to suggest that the Canada lynx synchronicity data among the eight provinces are also an indication of self-organization mediated by the spatial processes, i.e. dispersal and disturbance-modulated local dynamics.

The time-windowing technique, which is a central tool here, has its pros and cons. The technique calls for long enough time-series originating from several localities during a matching time-period. This is a far cry regarding long-term data on population dynamics, as most ecological time-series are short (much less than 100 years) and rarely replicated in space (Powell & Steele 1995). The Canada lynx data (Hewitt 1921; Elton 1924) are clearly an exception and, because of this uniqueness in temporal and spatial coverage, it is no wonder that they are still capable of producing new insights into population ecological processes (Royama 1992; Ranta *et al*. 1997*a*; Stenseth *et al*. 1999; Gamarra & Solé 2000).

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