

Spatially structured population dynamics in feral oilseed rape

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We studied the population dynamics of feral oilseed rape (*Brassica napus*) for 10 years (1993–2002) in 3658 adjacent permanent 100 m quadrats in the verges of the M25 motorway around London, UK. The aim was to determine the relative importance of different factors affecting the observed temporal patterns of population dynamics and their spatial correlations. A wide range of population dynamics was observed (downward or upward trends, cycles, local extinctions and recolonizations), but overall the populations were not self-replacing ($\lambda < 1$). Many quadrats remained unoccupied throughout the study period, but a few were occupied at high densities for all 10 years. Most quadrats showed transient oilseed rape populations, lasting 1–4 years.

There were strong spatial patterns in mean population density, associated with soil conditions and the successional age of the plant community dominating the verge, and these large-scale spatial patterns were highly consistent from year to year. The importance of seed spilled from trucks in transit to the processing plant at Erith in Kent was confirmed: rape populations were significantly higher on the ‘to Erith’ verge than the ‘from Erith’ verge (overall mean 2.83-fold greater stem density). Quadrats in which $\lambda > 1$ were much more frequent in the ‘to Erith’ verge, indicating that seed immigration can give the spurious impression of self-replacing population dynamics in time-series analysis.

There was little evidence of a pervasive Moran effect, and climatic forcing did not produce widespread large-scale synchrony in population dynamics for the motorway as a whole; just 23% of quadrats had significant rank correlations with the mean time-series. There was, however, significant local spatial synchrony of population dynamics, apparently associated with soil disturbance and seed input. This study draws attention to the possibility that different processes may impose population synchrony at different scales. We hypothesize that synchrony in this system is driven by at least three processes: small-scale, local forcing caused by soil disturbance, intermediate-scale forcing as a result of seed input, and large-scale climatic forcing (e.g. winter rainfall) that affects the motorway as a whole.

Keywords: oilseed rape; *Brassica napus*; spatial autocorrelation; disturbance; Moran effect; seed limitation

1. INTRODUCTION

The study of synchrony and spatial correlation in population dynamics has a long history (Elton 1924; Moran 1953; Kendall *et al.* 2000). Three potential causes of synchrony in population fluctuations over wide geographical areas have been identified: (i) environmental forcing (the ‘Moran effect’; see Koenig 2002); (ii) local, non-random dispersal (Royama 1992; Ranta *et al.* 1999; Bjornstad & Grenfell 2001); and (iii) predator–prey dynamics involving highly mobile, aggregating predators (Hassell 2000; Petty *et al.* 2000). Environmental stochasticity causes temporal fluctuations in the intrinsic rate of increase and/or carrying capacity of local populations that are correlated in space (but not time), with the environmental correlation typically decreasing with distance (Lande *et al.* 1999). Understanding the interplay between environmentally imposed randomness (‘noise’) and nonlinear population dynamics (‘signal’) is of considerable importance, especially for prescribing management of economically important or threatened species (Bjornstad *et al.* 1999; Grenfell *et al.* 2002).

Spatial synchrony in population dynamics (Kendall *et al.* 2000; Engen *et al.* 2002) has been reported for a wide variety of animal species including insects (Hanski & Woiwod 1993; Williams & Liebhold 2000; Bjornstad *et al.* 2002; Peltonen *et al.* 2002), feral sheep on islands (Grenfell *et al.* 1998), Svalbard reindeer (Aanes *et al.* 2003), caribou and musk oxen (Post & Forchhammer 2002), muskrat and mink across Canada (Haydon *et al.* 2001), grouse in Italy (Cattadori *et al.* 2000), freshwater fishes (Cattaneo *et al.* 2003), sea turtles (Chaloupka 2001) and diseases in towns (Bolker & Grenfell 1996). Regionally correlated climatic factors like rainfall, drought or extremes of winter temperature are also postulated as causing large-scale synchrony in the fluctuations of populations of short-lived plants (Hopkins 1978; Dunnett *et al.* 1998; Coomes *et al.* 2002) and synchronized time of flowering in several plant species over distances of up to 500 km (Post 2003).

This literature suggests that Moran effects are all pervasive, but there is no way of knowing the extent to which non-conforming cases have gone unpublished. Although the identification of factors responsible for key environmental forcing is an important application of time-series analysis, it is important to recall that in a nonlinear system, forcing at one temporal period can produce a response with

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variability at one or more different periods (Pascual & Ellner 2000). Equally, for plants like oilseed rape, where recruitment depends on soil disturbance to reduce levels of interspecific competition, it may be that the local, small-scale disturbance regime may be the main driver of population synchrony (Crawley *et al.* 1993, 2001).

Understanding spatial structure in transient systems also draws attention to the fact that the classic deterministic kernel of most theoretical models of population dynamics $N_{t+1} = \lambda N_t f(N_t)$ is not capable of dealing with time-series that include local extinctions ($N_{t+1} = 0$, $N_t > 0$) or colonizations ($N_{t+1} > 0$, $N_t = 0$; see Crawley & Brown 1995). In this paper, we analyse 3658 spatially structured 10 year time-series to investigate the factors affecting population synchrony; we detect roughly the same level of local synchrony (at scales of less than 1 km) as found for large-scale synchrony (*ca.* 180 km) that might be attributed to climatic forcing (i.e. a Moran effect).

2. METHODS

The 189 km verge of the M25 motorway is conveniently marked into numbered 100 m lengths, and we counted the number of flowering stems of oilseed rape within each 100 m stretch from a van travelling at the UK legal minimum speed (40 m.p.h.), in early May each year, from 1993 to 2002. There were 3658 quadrats in total (1829 in each verge), numbered clockwise from km = 5.0 on the southern shore of the Thames estuary, to km = 187.8 on the northern approaches to the Thames crossing. At 40 m.p.h., it was possible to count stems accurately up to *ca.* 16 per 100 m, but increasingly difficult thereafter (and impossible for numbers of more than 50). We therefore adopted a logarithmic scoring scheme, counting as follows: 0, 1, 2, 4, 8, 16, 32, 64 or 128+ flowering stems per 100 m. The clockwise carriageway was counted in the morning, then the procedure was repeated, counting the anticlockwise carriageway in the afternoon. Note was taken of the position of adjacent oilseed rape fields (to test for local seed dispersal), fields with oilseed rape volunteers from previous crops, and the presence of roadworks or other soil disturbance that might create suitable germination conditions for oilseed rape (Crawley *et al.* 1993). Oilseed rape typically grows within 1 m of the edge of the road and is seldom seen in dense grass or in deep shade. Details of the methods are in Crawley & Brown (1995).

We measured synchrony between 10 year time-series in two ways: by calculating Spearman's rank correlation coefficient across pairs of abundances in the two time-series; or by counting the number of coincident relative density transitions (i.e. synchronous ups, downs or stases) out of the nine observed transitions in the two time-series (Buonaccorsi *et al.* 2001). Population dynamics were modelled using nonlinear least squares to estimate the two parameters of the Ricker curve, $N_{t+1} = \lambda N_t \exp(-b.N_t)$. This function was chosen because of its flexibility in modelling a range of dynamics from stable equilibrium through cycles to chaos (see Dennis *et al.* 1998; Lele *et al.* 1998). The issues involved in fitting population models incorporating process noise and observation error are discussed by Pascual & Ellner (2000) and De Valpine & Hastings (2002). Only those time-series with four or more different oilseed rape densities were used for parameter estimation. Equilibrium $N^* = \ln(\lambda)/b$ is possible only for $\lambda > 1$ and $b > 0$.

Spatial patterns in mean density were investigated by calculating averages at a range of spatial scales from half of the motorway (95 km where $n = 2$ per verge per year) down to 1 km (where

$n = 187$ per verge per year) and calculating variance components for each scale using linear mixed effects models (Pinheiro & Bates 2000). Spatial autocorrelation functions were computed for each verge in each year, using the acf function in S-PLUS (Venables & Ripley 1997), and the autocorrelation at lag = 1 was plotted against year to investigate temporal trends in spatial structure. The only oilseed processing plant in southeast England is at Erith in Kent (national grid reference TQ 540760, close to km = 5 of the M25), and to test for the importance of rape seeds spilled in transit, we defined a two-level factor ('to Erith' and 'from Erith'), reflecting whether trucks on the road adjacent to the verge would be full of rape seeds or empty. We used an automatic journey planner (e.g. the route planner at www.theaa.com) to decide on the location of the split; it recommends travel to Erith by the clockwise carriageway when entering the M25 from the M40 (at km = 103) but by the anticlockwise carriageway when entering the M25 from the M4 motorway (km = 94), so we defined the split at km = 100.

Spatial correlation in population dynamics was assessed at a variety of scales. The simplest measure was Spearman's rank correlation between the 10 year time-series of rape densities in quadrats and their immediate clockwise neighbours. We also averaged the correlation coefficients over 2, 4, 8, 6, 10, etc. neighbouring quadrats. The spatial structure of 'synchrony hot-spots' (local regions with several adjacent significantly correlated time-series) was investigated by plots of correlation coefficient against distance, and its significance assessed by binomial tests, comparing observed and expected numbers of significant and non-significant correlation coefficients in different lengths of verge.

3. RESULTS

The 3658 individual quadrats exhibited a wide range of time-series, with some increasing, many decreasing, and others fluctuating regularly or irregularly. The time-series of overall mean density is shown in figure 1*a*, and the number of years out of 10 in which a quadrat supported one or more oilseed rape plants is shown in figure 1*b*. Permanently unoccupied quadrats numbered 411, but only 37 quadrats (*ca.* 1%) were occupied for the entire 10 year period. The most frequent pattern was for quadrats to have oilseed rape plants present for 1 or 2 years out of 10 (i.e. to show at least one local extinction followed by recolonization). The modal number of consecutive years of quadrat occupancy by oilseed rape was 1 year, the median was 1.5 years and the mean was 2.116 years (figure 1*c*). Regular cycles were shown in fewer cases than expected (there was only one case of 'down', 'up', 'down', etc., and four cases of 'up', 'down', 'up', etc., against an expectation of $3658/2^9 \approx 7$ each, supposing that all sequences of ups and downs were equally likely). Only two quadrats showed exactly the same pattern of ups and downs as was exhibited by the mean, and no permanently occupied quadrat had a constant population density over 10 years.

As described by Crawley & Brown (1995) for the period 1993–1994, and supported here for the full 10 year period, mean oilseed rape numbers were consistently higher in the verge adjacent to the carriageway taking trucks full of oil seeds to the processing plant at Erith in Kent than in the opposite verge (figure 1*a*). The difference between the two time-series was highly significant as assessed by a linear mixed effects model, with Erith as a fixed effect and years and verge-within-location as random effects

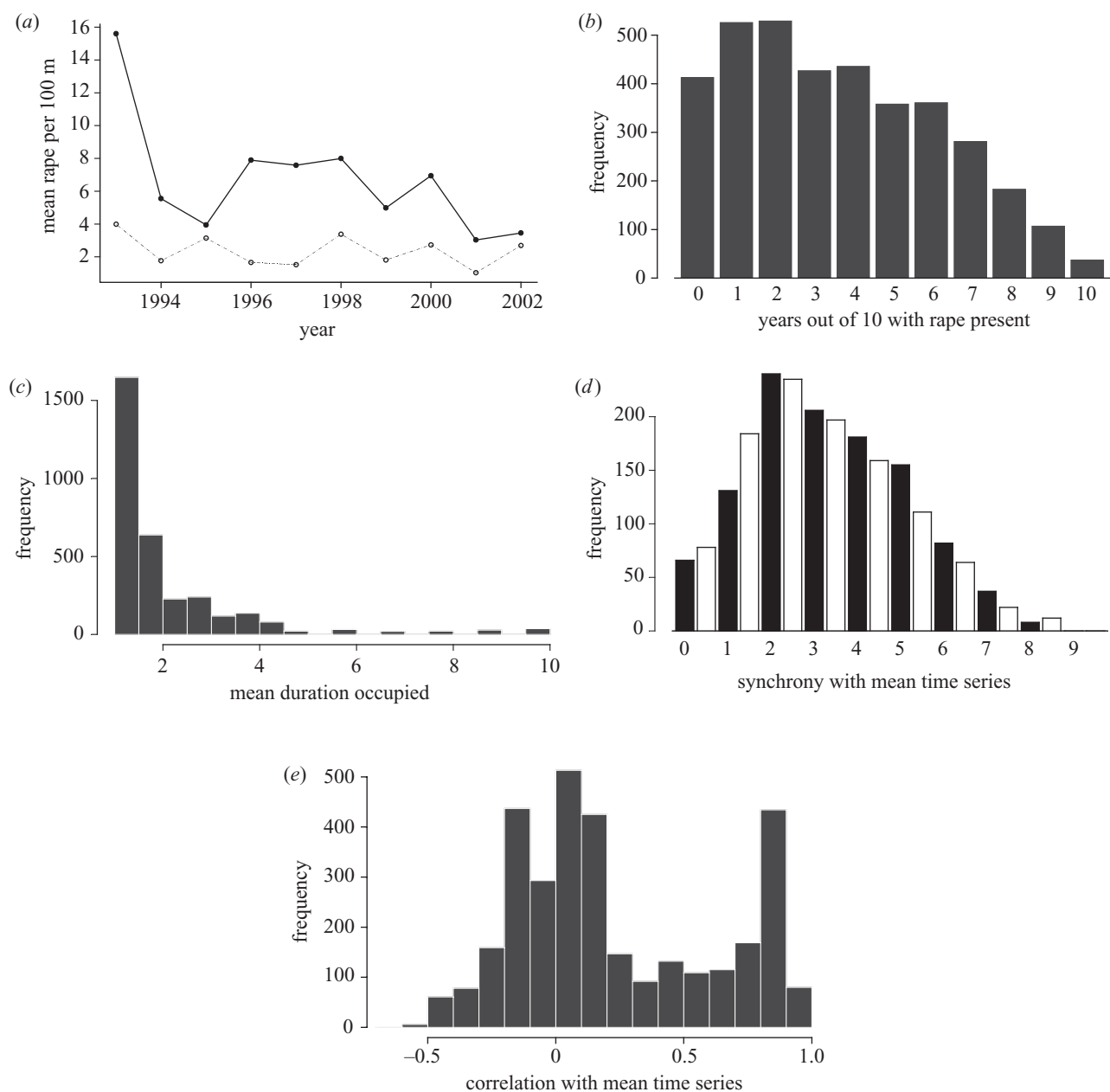


Figure 1. (a) Time-series for the populations of oilseed rape in the verges of the M25 motorway. Points are means over $n = 1829$ estimates of density in 100 m lengths of each verge in each year. Solid symbols, mean density on the verge adjacent to the carriageway taking trucks full of oil seeds to the processing plant at Erith in Kent; open symbols, mean density on the verge adjacent to the carriageway taking empty trucks away from Erith in Kent. The difference between the two time-series is highly significant (linear mixed effects model, mean difference = 4.403, s.e.m. = 0.203, d.f. = 1828, $t = 21.66$, $p < 0.0001$). (b) Time-series for 3658 quadrats summarized in terms of the number of years out of 10 for which oilseed rape was present (one or more plants). The most frequent cases were for quadrats to have oilseed rape plants present for 1 or 2 years out of 10. Permanently unoccupied quadrats numbered 413, but only 37 quadrats were occupied for the entire 10 year period. The most frequent pattern was for quadrats to show at least one local extinction followed by recolonization. (c) Mean duration (years) of quadrat occupancy for quadrats with 1 or more years of occupancy. The modal number of consecutive years of quadrat occupancy by oilseed rape was 1 year, the median was 1.5 years and the mean was 2.116 years. (d) Degree of synchrony between populations in the individual quadrats and the overall mean population (average of the two curves in (a)), measured by the number of matching inter-annual transitions (out of nine) that were both 'up' or both 'down'. Open bars, clockwise verge; solid bars, anticlockwise verge. (e) Correlation (Spearman's rank) between the mean time-series and each of the quadrats; 23% of quadrats were significantly correlated with the mean time-series at $p = 0.05$ ($r > 0.632$) and 17% at $p = 0.01$ ($r > 0.765$).

(mean difference = 4.403, s.e.m. = 0.203, d.f. = 1828, $t = 21.66$, $p < 0.0001$). The overall mean time-series was stationary for the 'from Erith' verge, but declined significantly over time on the 'to Erith' verge ($p < 0.05$, d.f. = 8).

We hypothesized that large-scale weather variables like rainfall or temperature might impose a substantial degree of synchrony in temporal dynamics across the area as a whole (a Moran effect). This issue was addressed by assessing synchrony (figure 1d) and correlation (figure 1e),

respectively. The most frequent class of quadrats showed just two transitions out of nine that were in step with the overall mean. Figure 1e shows a distinctly bimodal distribution of Spearman's rank correlation coefficients between the mean time-series and each of the quadrats; 23% of quadrats were significantly correlated with the mean time-series at $p = 0.05$ ($r > 0.632$) and 17% at $p = 0.01$ ($r = 0.765$); i.e. 77% of quadrats showed no significant correlation with the overall mean time-series. It is a moot point what the null expectation of synchrony or correlation should be for the acceptance of a Moran effect in a highly replicated system such as this, but it is evident that only a minority of quadrats fluctuated in synchrony (the appropriate null-distribution is the subject of ongoing research). Just one weather variable was correlated with overall mean rape density; total rainfall in February and March was negatively correlated with oilseed rape density counted in May of the same year ($r = -0.769$, d.f. = 8). The driest winter (1993 with 24.2 mm in February and March) coincided with the highest rape density, and the wettest winter (2001 with 212.5 mm) coincided with the lowest rape density. There was no correlation between total agricultural oilseed production in the previous year (www.defra.gov.uk) and mean rape population on the 'to Erith' verge ($r = -0.098$, d.f. = 8, n.s.), suggesting that fluctuations in the upper curve of figure 1a were not driven by country-wide fluctuations in agricultural production of oilseeds. There was no relationship between verge populations in year t , $t + 1$, or $t + 2$ and the presence of rape crops in adjacent fields ($p = 0.841$). Roadworks in year t were associated with significantly higher mean rape densities in year $t + 1$ and $t + 2$ in nine out of 12 cases where roadworks were evident at sampling time. The immediate effect of major roadworks was sometimes to reduce oilseed rape densities (e.g. when topsoil was removed completely) and sometimes to increase it (e.g. when there had been substantial soil disturbance in the previous autumn). After completion of roadworks, the subsequent course of oilseed rape abundance was somewhat more predictable. For instance, the section between km = 96 and km = 102 was under roadworks in May 1994. This section had low mean rape density in 1993 compared with flanking zones (km = 93–96 and km = 102–105), but rape density was more than four-fold higher in the year after the roadworks, but had returned to background levels after 4 years. The mean duration of oilseed population was longer after roadworks than on other parts of the verge (see above). A difficulty is that many important soil disturbances will have gone unnoticed because visits by machinery on the other 364 days of the year may have left no obvious trace on the day of the survey, and we were in no position to estimate the abundance of the kind of small-scale soil disturbances that create recruitment microsites for oilseed rape.

The 10 year population dynamics within each quadrat were assessed by fitting a Ricker curve to the nine density transitions in all cases where the data allowed ($n = 379$; see § 2). The overall dynamics were clearly not self-replacing, the mean recruitment curve lies everywhere beneath the replacement curve (figure 2a), and the mean value of λ was significantly less than 1 (overall $\lambda = 0.5731$; s.e.m. = 0.0133). Individual quadrats showed a wide range of values for λ , but the number of quadrats with $\lambda > 1$ was low (320 out of 3658). The quadrats with $\lambda > 1$ were

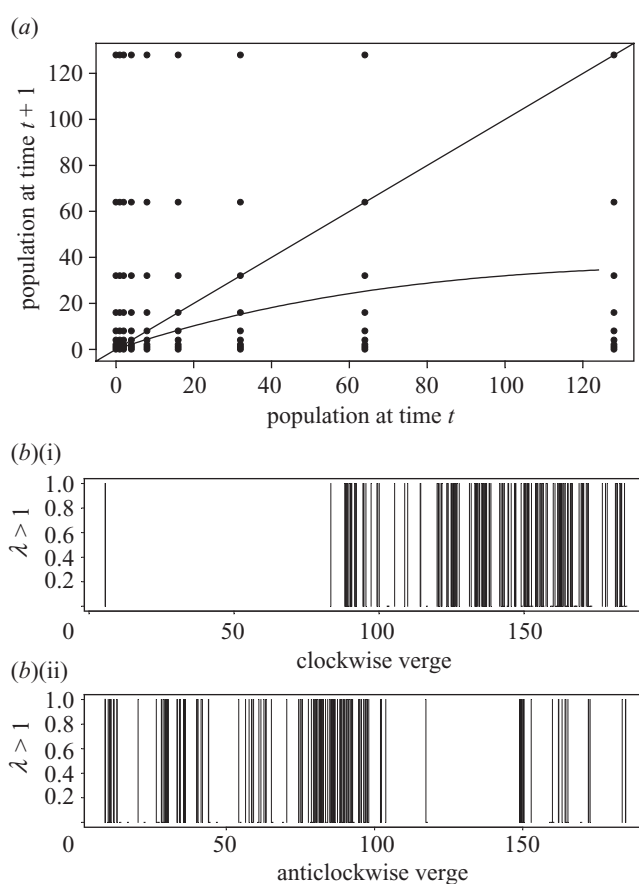


Figure 2. (a) Population dynamics of oilseed rape populations averaged over 10 years (nine transitions). Every possible transition in population size was observed at least four times (this rarest of transitions was from one plant in year t to 128 or more plants in the year $t + 1$). The most frequent transition was from no plants this year to no plants next year (frequency = 15 445). The straight line shows the replacement curve. The curved line is the nonlinear least-squares fit of the Ricker curve $N_{t+1} = \lambda N_t \exp(-bN_t)$ with parameters $\lambda = 0.5731$ (s.e.m. = 0.0133), $b = 0.00582$ (s.e.m. = 0.0002759). The recruitment curve lies everywhere beneath the replacement line, so there is no equilibrium, and populations tend to decline at all densities. (b) Locations of quadrats with $\lambda > 1$ are aggregated on the 'to Erith' parts of the (i) clockwise and (ii) anticlockwise verges.

significantly more frequent in the 'to Erith' than the 'from Erith' verge (the right-hand half of figure 2b(i), and the left half of figure 2b(ii); binomial test, $p < 0.0001$). We have no way of knowing the size of the seed bank in different quadrats, nor of estimating the rate of seed dispersal from adjacent quadrats. Likewise, there is no direct way of knowing the relative numbers of plants that were recruited from fresh seed, older seeds from the seed bank or immigrant seed.

We scored population density on a nine-point scale (from 0 to 128) so there were 81 possible density transitions for any quadrat from one year to the next. All 81 transitions were observed at one time or another, but some were much more frequent than others. Table 1 shows the 10 year mean probabilities for each of the 81 transitions, between population in year t (the rows) and year $t + 1$ (the columns). All entries in table 1 sum to 1.0 (whereas in a conventional transition matrix the rows would sum to 1). A

Table 1. The 10 year average probability of each of the 81 possible inter-annual density transitions.

(This year's populations (0 to 128) are represented by the rows, and next year's populations by the columns. There is a 47.6% chance that a square will be empty this year and empty again next year, and only a 0.22% chance that a square will be empty this year but support a population of 128 or more stems next year. Note that this is not like a standard transition matrix, where the row probabilities would sum to 1 and the figures would be the conditional probabilities of next year's population, N_{t+1} , given this year's population N_t .)

N	0	1	2	4	8	16	32	64	128
0	0.4758	0.0371	0.0366	0.0356	0.0286	0.0177	0.0065	0.0023	0.0022
1	0.0343	0.0034	0.0046	0.0050	0.0038	0.0024	0.0011	0.0002	0.0001
2	0.0350	0.0049	0.0047	0.0060	0.0063	0.0033	0.0016	0.0004	0.0002
4	0.0341	0.0051	0.0073	0.0095	0.0079	0.0071	0.0021	0.0006	0.0003
8	0.0276	0.0046	0.0060	0.0087	0.0091	0.0076	0.0030	0.0011	0.0005
16	0.0174	0.0031	0.0051	0.0063	0.0079	0.0083	0.0035	0.0013	0.0009
32	0.0073	0.0013	0.0015	0.0029	0.0035	0.0046	0.0023	0.0010	0.0007
64	0.0027	0.0004	0.0006	0.0011	0.0011	0.0018	0.0014	0.0008	0.0006
128	0.0015	0.0003	0.0002	0.0007	0.0008	0.0015	0.0010	0.0007	0.0017

striking feature of table 1 is that no matter what the population density at time t , the most frequently observed transition was to zero plants in year $t + 1$ (i.e. local, above-ground extinction). This is demonstrated by the fact that the transitions in the leftmost column of table 1 (i.e. the 'to zero' column) are always greater than any of the other transitions in the same row. By far the most frequent transition was from empty in year t to empty again in year $t + 1$ ($p = 0.4758$).

Spatial heterogeneity in mean oilseed rape density was evident at all spatial scales investigated. For example, analysis of variance compared mean densities when the whole verge was split into 2, 3, 4, 5, ... 179, 180 sections; each successive division explained a significantly greater part of the overall variation in rape density (results not shown here). Figure 3a shows the results for a division of the clockwise verge into 18 sectors each of 10 km in length (100 quadrats per sector). The increased plant density on the 'to Erith' verge is evident to the right of sector number 9. Likewise, figure 3b shows the results for the anticlockwise verge, where the sectors to the left of sector number 9 represent the 'to Erith' verge. There were temporal trends in the overall spatial structure of the local populations as assessed by the spatial autocorrelation coefficients; first order acf's were relatively constant (*ca.* 0.6) in the 'to Erith' verge, but increased from *ca.* 0.4 to *ca.* 0.7 in the 'from Erith' verge over 10 years.

Figure 4a shows the distribution of correlation coefficients between the time-series in one quadrat and the time-series in the quadrat immediately adjacent to it (clockwise); 18% of these were significant at $p = 0.05$. Calculating the mean correlation coefficient over the 10 adjacent quadrats (i.e. up to 1 km away) showed 22% of significant cases (results not shown). A striking feature of the data is the spatial aggregation of these significant temporal correlations (the dense clusters of vertical bars in figure 4b). Evidently there are hotspots of synchronicity as well as hotspots of mean density in both the clockwise and anticlockwise verges. Note, however, that high temporal synchrony was not associated with high local population density of oilseed rape ($p = 0.856$).

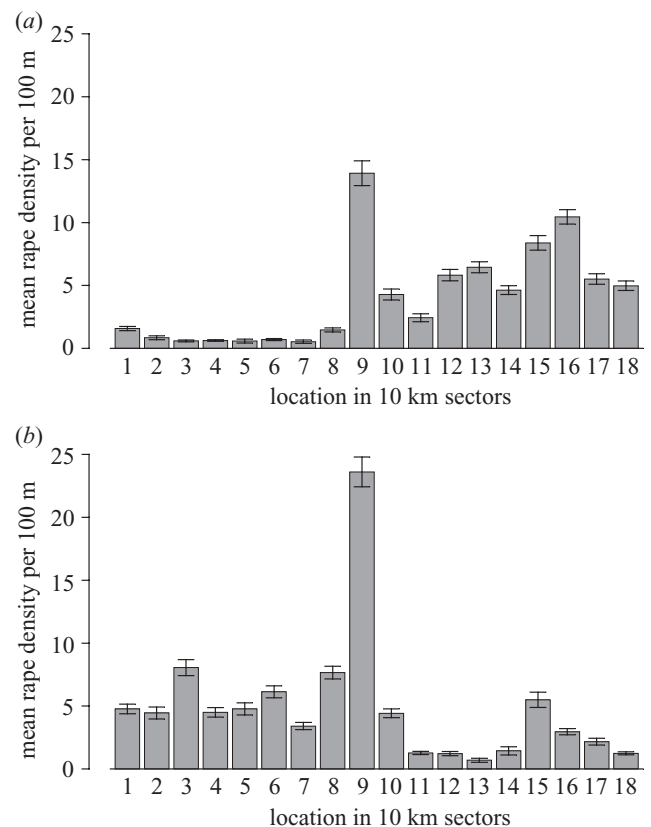


Figure 3. Spatial heterogeneity in mean oilseed rape density along the 189 km of the M25 motorway. Mean rape density per 100 m of verge. The location is a 10 km section of the verge, measured clockwise from km = 0 in the centre of the Thames Estuary near Erith. (a) Populations in the clockwise verge, (b) populations in the anticlockwise verge. Error bars show ± 1 s.e.m. ($n = 1000$, averaged over 100 quadrats and 10 years). There was significant heterogeneity at every spatial scale investigated from 95 km down to 100 m. In the clockwise direction, full lorries travelling towards Erith would enter at km > 100 (*ca.* location = 10) and move towards location = 18. In the anticlockwise direction, full lorries travelling towards Erith would enter at km < 100 (*ca.* location = 9) and move towards location = 1. The maximum populations are found in location 9 which is where the M25 motorway crosses the River Thames near Staines; here, large oilseed rape populations co-occur with large populations of native *Brassica rapa* subsp. *campestris*.

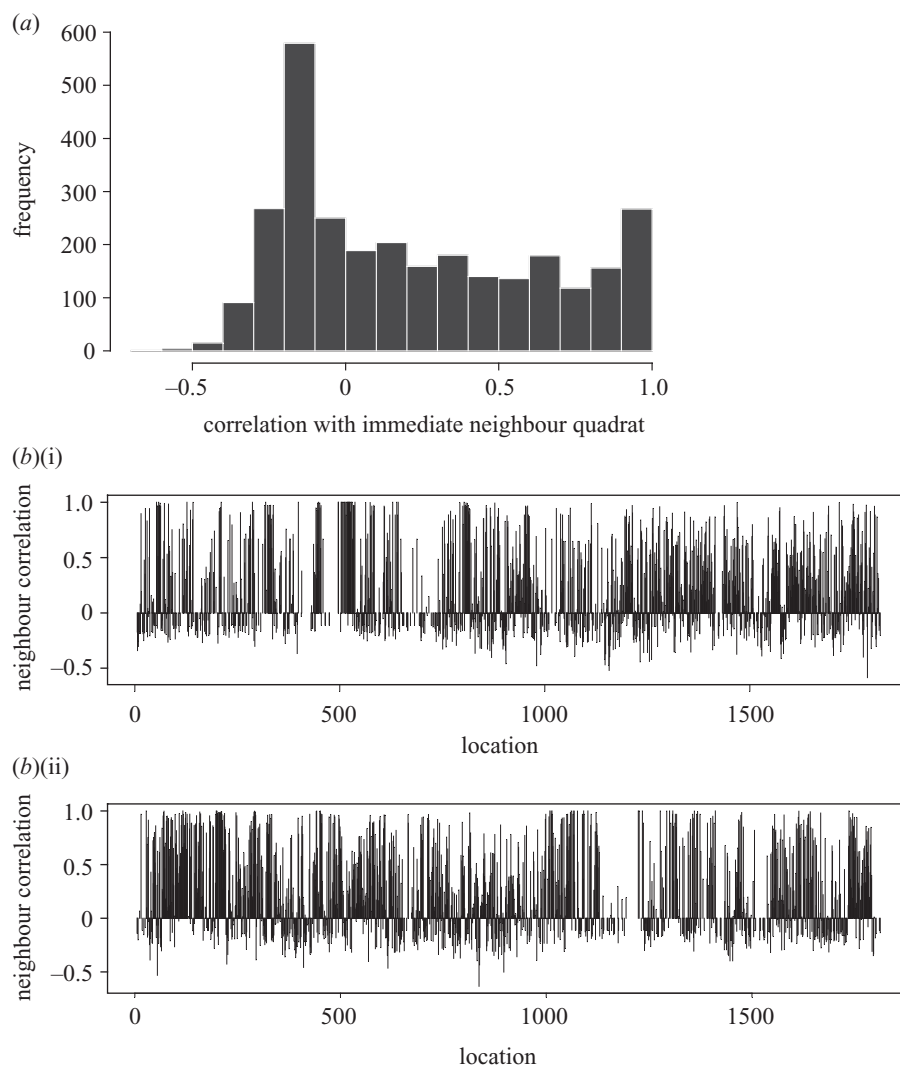


Figure 4. Spatial pattern in population dynamics. (a) Frequency distribution of Spearman's rank correlations between population time-series in one quadrat and in its immediate neighbour in the clockwise direction, showing a bimodal distribution in which most time-series were uncorrelated and *ca.* 18.11% were significantly correlated at 5%. (b) The spatial pattern of correlation in temporal dynamics: (i) the clockwise verge; (ii) the anticlockwise verge. White spaces show spatial runs of empty quadrats; although such neighbours were perfectly correlated in their dynamics, their lack of non-zero values meant that the correlation coefficient is computed as not available.

4. DISCUSSION

Oilseed rape showed a wide range of temporal dynamics over a 10 year period in 3658 quadrats adjacent to the M25 motorway (decreases, increases, cycles, extinction, recolonization, stasis, etc.). The most frequently observed pattern, however, involved classic 'casual' dynamics, with populations lasting for just 1 or 2 years before local extinction. 'Casual' is used here in the dictionary sense of 'occasional or irregular' with the implication that casual populations do not exhibit self-replacing dynamics (i.e. $\lambda < 1$), and rely on repeated introduction of seed for any semblance of permanence (Crawley 1997). The most likely cause of this ephemeral site occupancy is interspecific competition from perennial grasses, which eliminates microsites suitable for recruitment from seed (Crawley *et al.* 1993). Recruitment follows soil disturbance, and is boosted by seed spilled from lorries in transit to the oilseed processing plant at Erith in Kent (Crawley & Brown 1995). Local populations are forced into synchrony, therefore,

whenever several adjacent quadrats are disturbed simultaneously (e.g. during roadworks).

Just 23% of quadrats exhibited dynamics that were significantly correlated with the overall time-series of mean rape density, arguing against the existence of a strong, globally pervasive Moran effect (but more work is required on the null expectation, especially when so many quadrats were empty for the entire study period). Only one weather variable was significantly correlated with the overall mean time-series (namely total rainfall in February and March, which was negatively correlated with rape stem density in May; $r = -0.769$, $p = 0.0093$, d.f. = 8). We do not know the mechanism, but it is plausible that heavy winter rains might benefit the perennial grasses that are the principal competitors of oilseed rape.

There was substantial spatial heterogeneity in mean oilseed density at every scale investigated from 200 m to 100 km, and the spatial pattern in mean density was consistent from year to year over the study period. This reflects

broad differences in habitat suitability for oilseed rape, apparently because of soil conditions (lower densities on calcareous substrates) and successional stage (higher densities on recently disturbed, early successional ground, and virtual absence from older, dense grass swards). The most intriguing pattern, however, was the small-scale synchrony in population dynamics exhibited between neighbouring quadrats. The probable cause of this small-scale entrainment of population dynamics was soil disturbance by heavy machinery during road works, which simultaneously created patches of ca. 100–2000 m that were suitable for recruitment of rape from seed (data not shown).

We have no direct estimate of the strength of local density regulation (e.g. no detail on local seed production, germination or mortality), but where conditions are ideal (e.g. in places like sector 9 and sector 15, where *Brassica rapa* subsp. *campestris* is also abundant; figure 3), it is clear that population can exceed 250 flowering stems per 100 m quadrat, so intraspecific competition between adult plants is probably unimportant in most of our quadrats. Of course, this does preclude the possibility that there was intense intraspecific competition between seeds for access to suitable microsites; this could occur independently of adult density in the previous generation.

It is impossible with our data to quantify local seed dispersal (i.e. seed produced in one quadrat but dispersed to another), and hence to determine the role of local dispersal in generating small-scale synchrony in population dynamics (Royama 1992). It is clear, however, that planted fields of oilseed rape at comparable distances adjacent to the motorway were not a source of seed. There is always an interaction between local dispersal and environmental forcing, which means that dispersal and environmental correlation need to be considered in combination as explanations for observed patterns of population synchrony (Kendall *et al.* 2000).

It is interesting that populations which look, from time-series analysis, as if they exhibit self-replacing population dynamics (i.e. $\lambda > 1$ in nonlinear regression of Ricker curves) are disproportionately represented in the 'to Erith' verge of the motorway (figure 2*b*). Evidently, seed immigration can give the spurious impression of self-replacing dynamics in what is overwhelmingly an impermanent ('casual') system. Whatever the population of rape plants at time t , the most frequent density transition was to local above-ground extinction in year $t + 1$ (table 1).

There was no correlation between total agricultural oilseed production in the previous year and mean rape population on the motorway verge ($r = -0.098$, $n = 10$, n.s.), but there was a significant decline in mean density over time on the 'to Erith' verge. This may well be a result of improvements in seed containment in transit, because if it were a result of long-term ecological change (e.g. succession to dense grasslands) we should expect to observe a parallel decline in the 'from Erith' verge.

This study suggests that local forcing can be as important as large-scale environmental stochasticity (e.g. year-to-year climatic variability) in causing synchronous population dynamics. We hypothesize a hierarchy of several different forcing processes, each operating at a different spatial scale. Small-scale synchrony (over 200–1000 m) is caused by soil disturbance during road works and other off-road operations involving heavy machinery. Intermediate-scale

synchrony is enhanced by substantial inputs of seed, apparently spilled from trucks in transit. At the scale of the motorway as a whole, then climatic forcing (a classic Moran effect) may promote synchronous recruitment or mortality in widely separated quadrats where soil conditions and seed supply happen to permit.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.