

Increased outbreak frequency associated with changes in the dynamic behaviour of populations of two aphid species

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Sudden changes in the variability of natural populations can result in increased likelihood of extinction or in greater frequency and intensity of pest outbreaks. These changes could be associated with changes in some relevant population parameters such as the equilibrium density or the maximum population growth rate. However, changes in these parameters have very different consequences. An increase in equilibrium density results in a higher variance in population fluctuations according to the relationship between mean and variance described by Taylor's power law, but does not modify the stability properties of the system. On the other hand, changes in the maximum growth rate induce changes in the dynamic regimes and stability properties of the population. In this study, using statistical and mathematical methods borrowed from econometrics and engineering, we identify structural changes to the variance in the population dynamics of the sycamore aphid *Drepanosiphum platanoidis* and the green spruce aphid *Elatobium abietinum* in the UK. Some localities showed strong changes in their population parameters, such that their dynamic regime changed completely. These changes in the population dynamic regimes increase the expected frequency of outbreaks, which has enormous economic and ecological consequences. Through this study we show the application of methods that could be helpful to pest and wildlife managers in the task of evaluating changes in the risk of outbreaks or extinction of animal populations under changing global environmental scenarios.

Despite the wide body of evidence on the ecological effects of global change around the world (Stenseth et al. 2002, Walther et al. 2002), there is a high level of uncertainty about the potential responses of insect species to these changes. Insect populations have shown a variety of responses to these changes in terms of, for example, phenology, abundance and latitudinal and altitudinal ranges (Harrington and Stork 1995, Cannon 1998, Walther et al. 2002). However, another possible response of insect species to global change is a change in the temporal variability of population abundance fluctuations (May 1974, May et al. 1974, Hassell 1975, Hassell et al. 1976, Royama 1992). Sudden changes in the variability of natural populations can increase the likelihood of extinction (Ginzburg et al. 1982, Royama 1992, Schreiber 2001) or increase the frequency and/or intensity of pest outbreaks (Berryman and Millstein 1989, Berryman 1991, Turchin 1991, Cavalieri and Kocak 1994, Desharnais et al. 2001). Thus the question of how close the population is to a change in its dynamic behaviour is of interest to conservation biologists and pest managers. For example, aphids are among the most harmful insects to forestry and agriculture, and potential changes in their population dynamics related to global change have important consequences in pest management activities.

Population dynamics theory states that two hypotheses could explain a change in variability due to a change in the dynamics of a population. The first hypothesis explains the change in variability as a consequence of a change in the equilibrium (mean) density, in agreement with Taylor's power law relationship between mean and variance (Taylor 1961, Taylor et al. 1978, 1980). This law predicts that variance grows exponentially as a consequence of an increment in the long-term average population density. Therefore, if the limiting resource for a particular species increases, then it turns more abundant in an area, and it is expected that its variability also turns higher. The exact biological mechanism behind this law is still unknown, but behavior and demography have been proposed as potential explanation to this phenomenon (Soberon and Loevinsohn 1987). Under the second hypothesis, the change in variability is a result of a change in the maximum per capita population growth rate, inducing a switch towards more unstable population dynamics (May 1974, May et al. 1974, Hassell 1975, Hassell et al. 1976, Royama 1992). May (1974) showed how an increase in the maximum per capita growth rate leads to higher variances in the logistic model and, if the change is big enough, could even modify the dynamic behaviour of

the system from complete stability to damped oscillations, 2-point cycles and chaos. The increase in the maximum per capita growth rate is related to changes in the intrinsic birth (increase) or death (decrease) rates of the population. For example, it may occur if the individuals inside a population began to lay on average more eggs or to be more resistant to some mortality factor (or if that factor disappears). These hypotheses relate changes in variance to different population parameters. While the first is related to equilibrium density, the second is related to the per capita growth rate, and both may be tested by using population time series analysis (Royama 1992, Berryman 1999).

Long time series records of aphid species in the UK represent an opportunity to evaluate these hypotheses on the temporal variability of populations. In the last decade changes in the abundance of two species, the sycamore aphid *Drepanosiphum platanoidis* and the green spruce aphid *Elatobium abietinum* suggest a change in the pattern of variability in some localities. Previous studies showed that the population dynamics of green spruce aphids are partly the result of intra-population processes which cause a first-order and non-linear feedback structure in these aphid populations, which means that the abundance at time t mainly depends of abundance $t-1$ (Saldaña et al. 2007, Lima et al. 2008). However, these studies did not analyse the changes in variability in the last 10 years. In fact, predictions for years 1991 to 2005 obtained using models fitted to data from 1969 to 1990 show a poor match with real data in the localities where the variability in abundance has changed (Lima et al. 2008).

The consequences of an increment in population variability described previously make indispensable the incorporation and development of analytical tools for the detection and understanding of these changes. In this study, we introduce statistical and mathematical methods borrowed from econometrics and engineering, to show how the temporal variability of several aphid populations has experienced sudden changes over the last two decades. Although the development of these tools seems complicated, their implementation and use is simpler than other techniques available in the specialized literature (Yao 1988, McCulloch and Tsay 1993, Hawkins et al. 2003, Fearnhead 2006). Moreover, the interpretation of the results is directly related to population dynamics theory. We believe that these tools could be helpful for pest and wildlife managers in the task of assessing quantitative changes in the risk of outbreaks or extinctions of animal populations under global change scenarios.

Material and methods

Data

Records of aphids were taken from the 12.2 m suction trap (Macaulay et al. 1988) data of the Rothamsted Insect Survey (Taylor 1986, Harrington and Woiwod 2007). We used time series of the total number of aphids captured per year of two species: *Drepanosiphum platanoidis* and *Elatobium abietinum*. For *D. platanoidis* we used 11 localities in the UK (Broom's Barn, Hereford, Newcastle, Preston, Rothamsted, Starcross, Ayr, Dundee, Writtle, Wye and East Craigs) and, except for Writtle, the same localities were used for *E. abietinum*.

Time series cover 1966 to 2006, with years within this range depending on the locality. The shortest time series covers 29 years (Fig. 1). The trap network only records alate (winged) adult aphids. All active stages of *D. platanoidis* are alate when adult except for the sexual females (oviparae), and the species tends to show two major periods of flight activity in the UK, one in spring and one in autumn. The species has a quiescent stage in summer. *Elatobium abietinum* has a single period of alata production, with flight activity largely confined to late spring and early summer. For this species, suction trap records have been shown to be a good reflection of populations on trees (Day et al. 2010).

Detection of changes of variance

The algorithm developed by Inclán and Tiao (1994) was used to detect changes of variance. This algorithm uses the cumulative sums of squares (D_k) of a time series to identify retrospectively a change of variance. The central idea of this algorithm is that D_k (centred and normalized) has a Brownian bridge as an asymptotic null model. This means that, if the variance is constant through the time series (from 0 to t), then D_k at time 0 is equal to D_k at time t ($D_k(0) = D_k(t)$), and the limits to the variability of any time s $D_k(s)$, with $s < t$, is given by the conditional probability distribution of a Wiener process with the condition $D_k(0) = D_k(t)$. This structure makes that the maximum values of D_k are expected in the middle of the time series but are minimal at the extremes. If the expected limits are exceeded, the variance is not constant through the time series. In our case, when the realized value of D_k exceeds the 95% confidence interval for the expected maximum of the null model then this point is considered a true change of variance (boundaries in Supplementary material Appendix A3). However, to use this algorithm with ecological time series it is necessary to keep in mind some considerations. First, it is necessary to remove trends and autocorrelation from the time series. To remove trends, we replaced the original abundance data with the residual of the linear regression between the year and the abundance data plus the mean of abundances. To remove autocorrelation we used the residuals of an autoregressive model, AR(1), fitted to the detrended abundance data. Finally, due to ecological time series being too short to use the asymptotic confidence intervals of the null model, the observed D_k values were multiplied by $\sqrt{T/2}$, where T is the length of the time series, for comparison with the asymptotic boundaries (Inclán and Tiao 1994). We provide an R code for the calculation of D_k statistics in Supplementary material Appendix A4.

The model and regime switch thresholds

A non-linear version of the Ricker model of population dynamics (Ricker 1958) was used as a baseline to examine the fluctuation patterns of both aphids. This model, based on a difference equation, has been used successfully in the modelling of aphid species, even with *E. abietinum* (Saldaña et al. 2007, Lima et al. 2008, Estay et al. 2009), and it has been extensively studied, which facilitate our analytical approach. Despite this, any population dynamics model may be used to achieve our objective following the next reasoning.

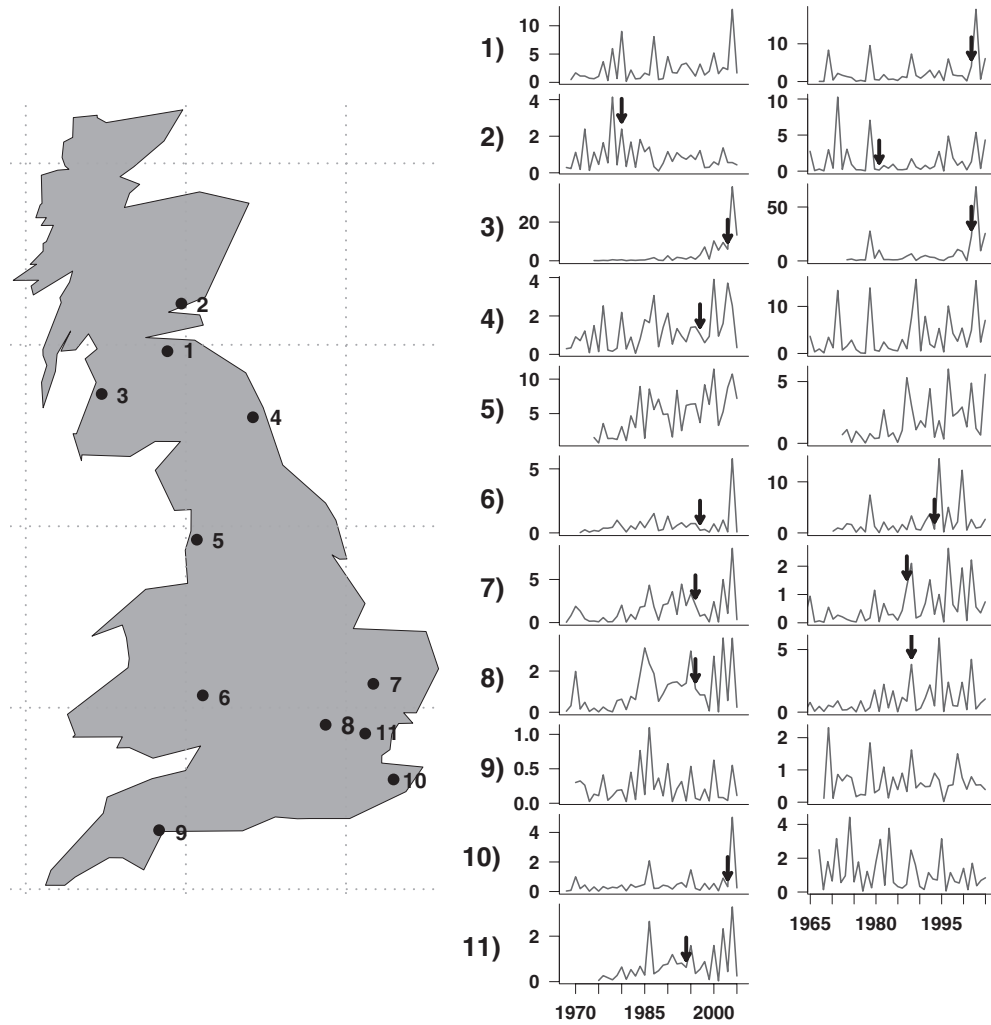


Figure 1. Map of the 11 localities in the UK and the time series of aphid abundances. Left column: *D. platanoidis*. Right column: *E. abietinum*. The localities are 1) East Craigs, 2) Dundee, 3) Ayr, 4) Newcastle, 5) Preston, 6) Hereford, 7) Broom's Barn, 8) Rothamsted, 9) Starcross, 10) Wye, 11) Writtle. Arrows mark the approximated moment where the change of variance occurred. Due to scale effects in the images, the changes of variance are better visualized in the supplementary information.

The model is:

$$R = R_m \left(1 - \left(\frac{N_{t-d}}{K} \right)^Q \right) \quad (1)$$

where N_{t-d} is the abundance at time $t - d$; R is the realized per capita growth rate $R = \ln(N_t/N_{t-1})$; R_m is the maximum per capita growth rate estimated for the species; K is the equilibrium density and Q is a nonlinearity factor (Berryman 1999).

The linear version of this model,

$$R = R_m \left(1 - \frac{N_{t-1}}{K} \right) \quad (2)$$

was analysed in detail by May (1974). The dynamic behaviour of the linear version in the equilibrium depends on one parameter, R_m . May (1974) demonstrated that when $0 < R_m < 1$ the system approaches the equilibrium (K) monotonically; if $1 < R_m < 2$, then the system approaches

the equilibrium with damped oscillations; if $2 < R_m < 2.526$ the system has a 2-point cycle, and so on (see the threshold values in May 1974).

In the non-linear version, the dynamic behaviour in the equilibrium depends on two parameters, R_m and Q .

The R-function,

$$R = \ln \left(\frac{N_t}{N_{t-1}} \right) = R_m \left(1 - \left(\frac{N_{t-1}}{K} \right)^Q \right) \quad (3)$$

evaluated in the equilibrium, depends on the function $Q \times R_m$ (slope). Then, in order to obtain the functions in the $Q - R_m$ parameter space that describes the thresholds where the dynamic behaviour changes, we followed the procedure of May (1974) and Hassell (1975).

The function $Q \times R_m$ is assumed to be equal to every threshold value of the linear version of the model, $Q \times R_m = a$, where a is the threshold of the linear case (1, 2, 2.526, ..., etc). Then, the functions describing the limits of areas of monotonic damping, damped oscillations

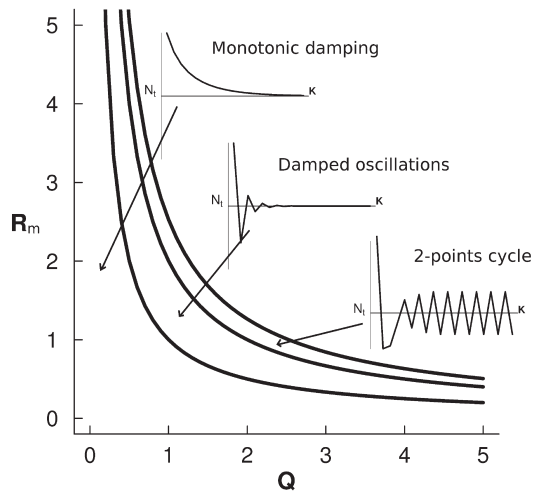


Figure 2. $Q - R_m$ parameter space and thresholds for the Ricker model. The first three regimes are shown. Each curve represents a threshold with the form a/Q .

and 2-point cycles in the $Q - R_m$ parameter space are: $R_m = 1/Q$, $R_m = 2/Q$ and $R_m = 2.526/Q$, respectively (Fig. 2). Therefore, all functions describing thresholds have the general form $R_m = a/Q$.

Using the records of the two aphid species from the Rothamsted Insect Survey we estimated R_m , K and Q for each location. The models were fitted by non-linear least squares using the `nls` library in the R program (R Development Core Team 2008).

Minimum distance between observed parameter values and thresholds

Once the change of variance is detected, two possible scenarios arise: whether the change in variance involves or not a change in the stability properties of the system. The answer could be found in a careful examination of the change in population parameters. Because, at least theoretically, R_m , K and Q show a tradeoff in their expected values (Johst et al. 2008, Pastor 2008), a unique measure of change in the parameter values in relation to the threshold is needed. We use the minimum distance to threshold (MDT) as a measure of change in the stability of the system and, therefore, in the variance of the series. The central idea is that, if the change of variance is due to a change in dynamic properties of the system, then the minimum distance between the combination of the estimated parameters R_m and Q to some of the thresholds in the parameter space (Fig. 2) should be lower after than before the change of variance. For example, if we plot the values of R_m and Q obtained from the fitting of a Ricker's model in the graph of Fig. 2, and the point is somewhere below the first threshold curve, then the endogenous variance in the long-term is zero and the observed variance corresponds to environmental noise. If the combination of parameters is above the first curve but below the second curve, then the endogenous variance in the long term is higher as the distance to the second threshold curve diminishes, and so on. Therefore, a decrease in the MDT implies

an increase in the variance of the time series due to a change in the stability of the system (parameters R_m and/or Q), and not to due to an increase in K . In the case of a change of variance associated with parameter K , MDT should not be significantly reduced after the change, because K does not alter the dynamic regime and hence MDT would not show important changes. Details of how MDT is obtained are in the supplementary information, Supplementary material Appendix A1.

To evaluate the MDT, first all the series that showed a change of variance according to the algorithm of Inclán and Tiao (1994) were divided at the point where the algorithm detected the break. If there were enough points each side of the break (at least eight points in each segment), the data in each segment were used to estimate the parameter values for a non-linear Ricker model (Eq. 3). Given the strong concave form of the data, we estimated the R_m parameter using cubic splines and bootstrapped the procedure to avoid convergence problems. Once parameter values were estimated for each segment, we calculated the MDT for each of them. As stated before, we expect that those changes in variance associated to changes in the stability properties of the system will show a significant change in MDT as a result of changes in parameters R_m and/or Q . On the contrary, those changes in variance that are not associated to changes in the stability of the system will show no significant changes in MDT, as a result of changes in parameter K . Thus, the identification of change points in variance, together with the estimation of changes in MDT allow the discrimination of potential causes of shifts in population variability. All analyses were performed in R environment. To calculate MDT, a user-friendly spreadsheet application is available from the corresponding author for interested readers.

Results

The algorithm of Inclán and Tiao (1994) detected that 60% of 21 analysed time series showed changes of variance; 6 of 10 populations of *Elatobium abietinum* and 7 of 11 populations of *Drepanosiphum platanoidis*. In the case of *E. abietinum* the localities of Broom's Barn, Hereford, Rothamsted, Ayr and East Craigs showed an increase and Dundee a decrease in variance (Table 1, Fig. 1). In the case of *D. platanoidis*,

Table 1. Locations and years where a change of variance was detected according to the algorithm of Inclán and Tiao (1994). NA means no change was detected.

<i>E. abietinum</i>		<i>D. platanoidis</i>	
Location	Year	Location	Year
Broom's Barn	1988	Broom's Barn	1996
Hereford	1995	Hereford	1997
Newcastle	NA	Newcastle	1997
Preston	NA	Preston	NA
Rothamsted	1989	Rothamsted	1996
Starcross	NA	Starcross	NA
Ayr	2003	Ayr	2003
Dundee	1982	Dundee	1980

Broom's Barn, Hereford, Newcastle, Rothamsted, Ayr and Wye showed an increase and, again, Dundee a decrease in variance (Table 1, Fig. 1). The year when each change occurred in each locality is shown in Table 1.

Just four populations of *E. abietinum* and five of *D. platanoidis* had enough points to calculate MDT according to the criteria explained in the methods section (at least eight points in each time series segment). In *E. abietinum* we used Broom's Barn, Hereford, Rothamsted and Dundee; the same localities plus Newcastle were used with *D. platanoidis*. The estimation of population parameters is shown in Table 2. For *E. abietinum* only Broom's Barn underwent a decrease in the MDT (threshold $2/Q$, Fig. 3, Table 2). The decrease in MDT at Broom's Barn is mainly due to an increase in R_m after 1988, whereas at Rothamsted and Hereford the change in variance is due to an increase in K and Q without a significant change in MDT (Fig. 3, Table 2). In the case of the reduction of variance at Dundee in 1982, this seems to be located just between 1982 and 1993, after this year the population reassumed the pattern of fluctuations previous to 1982.

The results for *D. platanoidis* (Fig. 4) have a more consistent pattern than for *E. abietinum*. In the five populations analysed a change in the MDT is responsible for the change of variance, and two of these populations showed a regime switch (threshold $2/Q$, Fig. 4, Table 2). Broom's Barn and Rothamsted showed an abrupt decrease of MDT mainly due to an increase in R_m after 1996, which changed the regime of monotonic damping to damped oscillations, and in the case of Rothamsted almost to a 2-points cycle regime (Fig. 4). Hereford also showed an abrupt reduction of MDT due to an increase in R_m , but without a regime switch in 1997, but Newcastle had a change of variance due to an increase in K (Fig. 4, Table 2). Dundee underwent a decrease in R_m which reduced the amplitude of the oscillations after 1980 (increase of MDT, Table 2).

Interestingly, we did not detect a change in the time series for Writtle, mainly due to an outbreak in 1986. However, if we remove this point, the change of variance is clear, resulting in a reduction of MDT and the population parameters change in the same way as for Broom's Barn, Hereford and Rothamsted, with an abrupt increase of R_m after 1994 (Fig. 4, Table 2). Details of detected changes of variance as well as for calculated MDT for each species and locality may be found in the supplementary information, Supplementary material Appendix A2.

Discussion

Our analyses reveal that changes of temporal variability seem to be a common phenomenon in aphid populations in the last 20 years. At least 60% of the analysed populations in each species showed this kind of change, especially in the 1990s.

Observed changes in population dynamics of *Elatobium abietinum* and *Drepanosiphum platanoidis* are commensurate with theoretical predictions of change in variance. The changes of variance in *E. abietinum* corresponded to an increment in the equilibrium density (K) without a change in the maximum reproductive rate (R_m), with the exception

Table 2. Estimated model parameters and MDT for each species and locality before and after the changes of variance. Between brackets the 95% confidence interval for the estimation. *means a regime switch for this locality.

Location	Before			After			MDT	
	R_m	K	Q	R_m	K	Q	Before	After
a) <i>E. abietinum</i>								
Broom's Barn	2.01 [0.32–3.32]	25.35 [13.47–40.65]	0.64 [0.36–1.02]	3.13 [0.98–4.30]	70.81 [39.90–108.54]	0.47 [0.27–0.72]	0.32	0.17
Hereford	3.39 [2.61–4.12]	113.35 [61.83–191.01]	0.37 [0.21–0.54]	2.22 [1.02–3.44]	233.77 [119.42–400.15]	0.59 [0.39–0.86]	0.22	0.29
Rothamsted	3.20 [2.30–3.89]	45.65 [26.48–70.26]	0.48 [0.30–0.70]	2.50 [1.24–3.65]	121.47 [84.62–165.29]	0.69 [0.52–0.91]	0.14	0.1
Dundee	2.26 [0.05–4.57]	66.14 [0.00–159.12]	0.40 [0.13–0.66]	2.55 [0.76–4.42]	78.23 [31.30–125.16]	0.42 [0.23–0.61]	0.04	0.03
b) <i>D. platanoidis</i>								
Broom's Barn*	1.80 [0.61–2.72]	1128.49 [258.89–1198.09]	0.38 [0.08–0.69]	3.31 [0.81–4.68]	1352.40 [26.43–2678.38]	0.43 [0.12–0.74]	0.65	0.17
Hereford	1.87 [0.70–2.48]	481.02 [312.75–674.34]	0.56 [0.31–0.86]	3.63 [1.36–6.11]	462.40 [0.00–938.50]	0.36 [0.17–0.55]	0.45	0.19
Rothamsted*	1.68 [0.09–2.67]	720.73 [0.00–1503.95]	0.30 [0.00–0.60]	4.84 [3.52–5.38]	962.68 [407.91–1767.88]	0.42 [0.21–0.72]	0.77	0.01
Newcastle	2.39 [0.65–3.22]	876.91 [577.66–1209.33]	0.55 [0.37–0.82]	2.36 [0.25–4.18]	1747.08 [791.81–2702.27]	0.58 [0.12–1.04]	0.27	0.25
Writtle	1.48 [0.00–2.10]	565.61 [292.36–978.60]	0.57 [0.26–0.91]	3.41 [2.31–4.23]	761.95 [394.35–1249.81]	0.50 [0.28–0.77]	0.63	0.09
Dundee	2.35 [1.22–3.28]	924.38 [475.50–1569.05]	0.59 [0.33–0.93]	1.47 [0.00–2.55]	783.63 [568.30–1006.14]	0.78 [0.49–1.11]	0.25	0.46

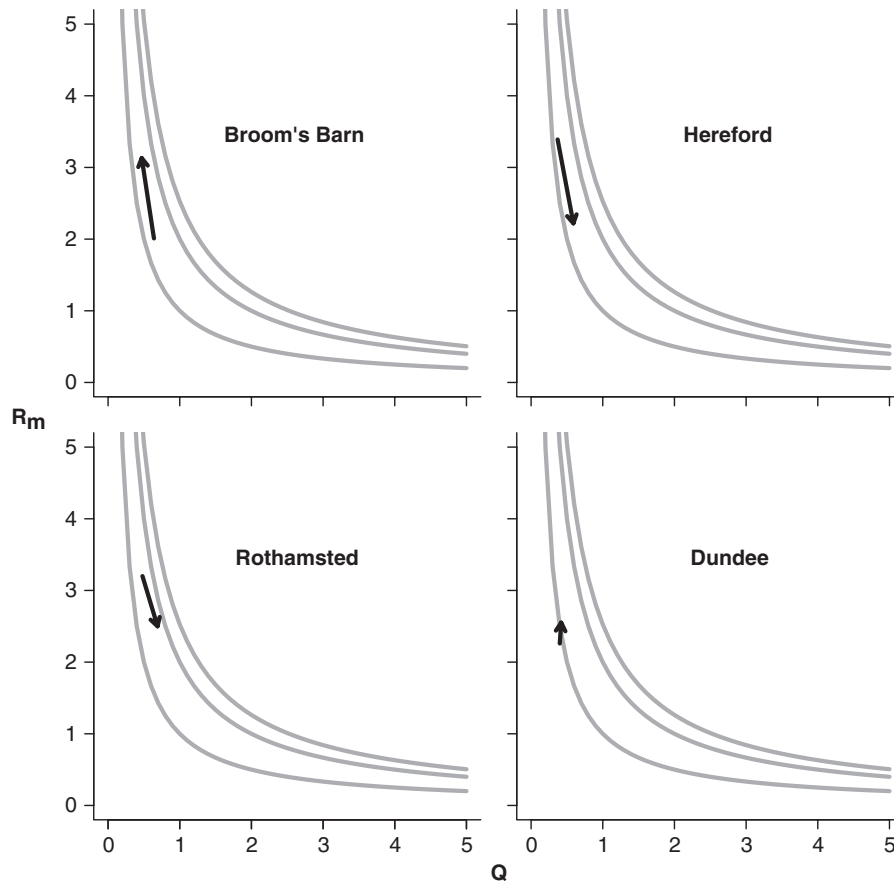


Figure 3. MDT statistics for *E. abietinum*. Arrows begin in the parameter combination previous to the change of variance and end in the parameter combination after the change of variance. See Table 2 for specific values.

of Broom's Barn. According to this result, the more probable reason for these changes is an increment in the availability of a limiting resource for the population which means that the aphid is more abundant now than in the past decades. This kind of effect does not have consequences for the dynamic behaviour of the system because, despite the increment in variance as Taylor's power law predicts, the parameter K theoretically does not have influence on the stability of the population process (May 1974, May et al. 1974). This situation is corroborated by the minimal changes in MDT at Hereford, Rothamsted and Dundee (Table 2) which imply no important dynamical changes in the system. However, at Broom's Barn this species showed an important reduction in MDT mainly due to the strong increase in R_m (from 2.01 to 3.13), which means that in this locality the endogenous variability of the system increased in recent years.

In *D. platanoidis* the observed changes of variance are mainly associated with changes in R_m , with the associated changes in dynamic regime. This suggests that either the current environmental conditions are more favourable for reproduction or some important mortality factor reduced its intensity. As seen in Table 2, most populations of *D. platanoidis* showed an increment in R_m after the change of variance. With the exception of Newcastle, which showed no change in MDT but an increase in the parameter K , all localities with enough points to test it showed a strong decrease in MDT, due mostly to an increase in R_m , which implies an

increase in their endogenous variance. These reductions in MDT were strong enough to change the dynamic regime from monotonic damping to damped oscillations at Broom's Barn, Rothamsted and Writtle (Fig. 4, Table 2). These regime switches may have important ecological and economic consequences. The increase in variance results from much higher densities during the peaks of the fluctuations rather than from lower densities during troughs. In this scenario, years with high abundances of these aphids will be more frequent, and the pressure exerted on the host trees could have serious consequences for the forest ecosystems (Carson and Root 2000, Volney and Fleming 2000, Hunter 2001).

Considering the simultaneity of the changes detected in this study, we can speculate that a potential candidate to induce these changes is an environmental force operating at a large geographic scale. Despite the identification of this force being beyond the scope of this study, we can speculate a little about its nature and characteristics. First, observed changes of variance are abrupt in all time-series, which suggests a non-linear reaction of the system to the change and, second, this environmental force should have known effects on the parameters R_m , Q and/or K . Among all environmental forces, weather is the iconic example that satisfies these characteristics. The influence that variables such as temperature and relative humidity have on population parameters is historically known (Holdaway 1932, Frazier et al. 2006), and it is valid to suppose that

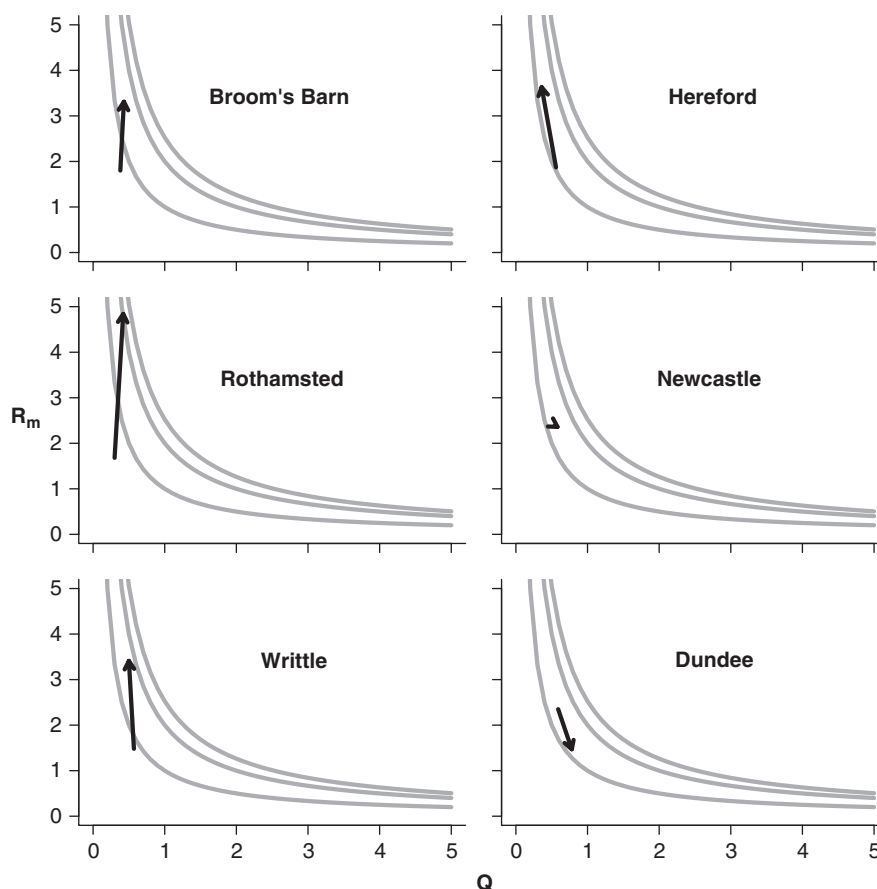


Figure 4. MDT statistics for *D. platanoidis*. Arrows begin in the parameter combination previous to the change of variance and they end in the parameter combination after the change of variance. It is clear how in Broom's Barn, Rothamsted and Writtle populations the regime changes from monotonic damping to damped oscillations and how MDT strongly decreases in relation to the second threshold. See Table 2 for specific values.

under the current changing climate non-linear effects on the patterns of population fluctuations may emerge (Martinat 1987, Wellings and Dixon 1987, Porter et al. 1991, Cammell and Knight 1992, Huey and Berrigan 2001, Harrington et al. 2007). For example, the North Atlantic Oscillation has exhibited a positive trend in the last decades (Gillet et al. 2003) which could modify several ecological processes in UK or northern Europe (Ottersen et al. 2001) including changes in the pattern of precipitation of temperature that have a known effect on the survival of aphid species. In other examples, Powell and Perry (1976), Bale et al. (1988) and Lima et al. (2008) showed how extreme cold events increase the mortality of different aphid species in the field, and in this way modify parameter R_m . A fall in the intensity, frequency or opportunity of these extreme cold events could have induced the changes observed in our study. On the other hand, Estay et al. (2009) showed how precipitation intensity modifies the equilibrium density (K) of the aphid *Tuberculatus annulatus* in the UK. These examples highlight the consequences that the current climate change could have not only on averages population sizes, but also on their variability. In the context of our methodological proposal, the estimation of MDT and its change in time could be useful to relate changes in environmental conditions to the stability

properties of the population system. For example, changes in MDT in these aphids could be related to changes in average environmental conditions (temperature, humidity, CO_2 , host availability, etc) or to changes in the frequency of extreme events. To determine a relationship (linear or nonlinear) between the change in any environmental variable and changes in MDT would suggest that environmental change drives changes in population stability.

The methodological tools used in this study could be applied retrospectively to understand causes of past changes. Calculating MDT at several intervals or windows time in a population time-series allows us to track trends in population parameters in a similar way as Bierman et al. (2006) and Saitoh et al. (2006) did with time-series of several populations of rodents with multi-annual cycles. MDT may be a useful tool to track parameter changes and a good indicator of future changes in the dynamics based on its observed current trend assuming all else being the same. Despite the fact that this kind of analysis is not prospective *sensu stricto* (Caswell 2000) and requires long-term data, it may provide some valuable insights about future trends in the dynamics of populations with relatively short ecological time-series (10–15 years).

The Inclán and Tiao algorithm is not the only technique available to detect changes of variance in time series. Other techniques based on different principles are available in the

specialized literature. These include among others, control charts (Hawkins et al. 2003), Bayesian posterior odds (Fearnhead 2006) and penalized likelihood methods (Yao 1988). All these are examples of techniques that allow the detection of changes of variance in long time-series. In ecological context, these techniques have been used in oceanographic data (Killick et al. 2010). However, it must be noted that the data set used by Killick et al. (2010) is one order of magnitude greater than the longest time series available for aphid populations, which are among the best studied population time series available to ecologists. This highlights the fact that most of these alternative techniques require long time series. Also, it is necessary to evaluate how these techniques may be applied to autocorrelated data such as abundance data, and whether the autocorrelation structure of these time series affects the detection of variance changes. Addressing both the constraints of time series length and potential biases of autocorrelated time series are research questions that must be dealt with in order to allow a broader application of these techniques to ecological population time series. Hence, an important degree of work is required to ensure correct implementation and application of these methods to systems with scarce data.

The population phenomena analysed in this study have economic implications. The expected higher number of aphids means an increase in the frequency of outbreaks in these localities or at least a higher number of times in which the economic injury level will be exceeded. Through this study we were able to test theoretical predictions about the expected dynamic changes in population systems using long-term data. Furthermore, we showed how theoretical insights from different branches of population ecology explain the abrupt changes that aphid populations underwent in the last decades, which is the base for the future development of management guidelines, one of the major goals of applied ecology.

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Supplementary material (available online as Appendix O19525 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A4.

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