

QÜESTIÓ, vol. 21, 1 i 2, p. 269-272, 1997

SOME UNRESOLVED ISSUES IN NON-LINEAR POPULATION DYNAMICS

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The Lyapunov exponent is a statistic that measures the sensitive dependence of the dynamic behaviour of a system on its initial conditions. Estimates of Lyapunov exponents are often used to characterize the qualitative population dynamics of insect time series. The methodology for estimation of the exponent for an observed, noisy, short ecological time series is still under development. Some progress has been made recently in providing measures of error for these exponents. Studies that do not account for noise when reconstructing the dynamics of series must remain questionable.

Keywords: Chaos, population dynamics, non-linear dynamics, time series, Lyapunov exponent, randomization, aphids, moths.

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–Article rebut el febrer de 1997.

–Acceptat el juny de 1997.

Ecological time series concerned with the population fluctuations of organisms are usually short, consisting typically of no more than 30 generations, and often fewer. Such series are often based on counts, and estimate the population density of an insect population, once per generation. The data are therefore not continuous, but discrete. The populations they represent are often distributed exceedingly patchily, and frequently include many zero values. By contrast with physical variables, such populations are highly dynamic, and have usually evolved to shift ceaselessly in space and time for ecological reasons. They are often characterized by isolated clusters, which may be acting as metapopulations with varying degrees of inter-cluster dispersal (Perry & González-Andújar, 1993).

Turchin & Taylor (1992) proposed that the dynamics of ecological time series be represented by a response surface, with a dependent variable of logarithmically-transformed growth rates and with several independent variables, each a function of a lagged variable, i.e. a count from a previous generation. Their proposals were examined by Perry, Woiwod & Hanski (1993), who objected on various statistical grounds, pointed out difficulties over robustness, and presented alternative models. Both of these papers made predictions of the qualitative nature of the underlying, endogenous dynamics, by fitting the surface and inspecting the time series reconstructed from the deterministic skeleton represented by the estimated surface parameters. The behaviour of this time series, predicted for hundreds of generations into the future, was used to characterize the dynamics underlying the observed data.

However, this approach was severely criticized by Ellner & Turchin (1995), who emphasized that the previous methods were flawed because they did not allow for a random component in the dynamics, and this could lead to non-chaotic series being misidentified as chaotic. Ellner & Turchin (1995) identified three sources of variation that might influence the sensitivity of the system to initial conditions, namely: endogenous dynamics, exogenous dynamics and measurement error, and pointed out that fluctuations cannot be categorized as stochastic or dynamic by methodology that assumes the absence of noise. As an alternative, they suggested that dynamics should be characterized directly through the Lyapunov exponent, and presented Jacobean methods for calculation of the Lyapunov exponent that allow for dynamic noise. While this new methodology cannot disentangle the relative contributions of measurement error, which is usually assumed to be small, from exogenous dynamics, it does identify the effects of the exogenous dynamics, which is usually the aim of the exercise. Unfortunately, it is not easy to provide standard errors or measures of variability for such estimates. Although positive Lyapunov exponents indicate chaotic dynamics, positive values close to zero might occur due to measurement error, and the series might have a true value of zero, indicating quasiperiodic dynamics or a negative value, indicating stability. Furthermore, it is impossible to rely on theory or asymptotic results to supply measures of variability.

Zhou *et al.* (1997) provided some measures by using a randomization technique pioneered by Pollard, Lakhani & Rothery (1987), from the density dependence literature. Essentially, the series counts or growth rates are permuted under certain null hypotheses, and a randomization distribution of Lyapunov estimates built up from these permutations against which the observed value may be assessed. The advantage is that the approach is non-parametric and, much in the spirit of bootstrapping, uses the observed data and avoids the need to make too many, possibly dubious, assumptions. The disadvantage is that the variability of the randomization distribution is of interest only if the null hypothesis is plausible. Zhou *et al.* (1997) considered two null hypotheses. One, that the population undergoes complete compensation in the next generation for any exogenous density fluctuations suffered during the current one, is of interest as an extreme baseline, but is hardly likely to hold for any species in practice (Hanski, Woiwod & Perry, 1993). The other, that the population is behaving in a purely density-independent fashion, is more likely, and indeed is one possibility proposed in a debate that been waged in ecology for forty years. However, it is now thought much less likely than used to be the case, for the majority of species (Woiwod & Hanski, 1992).

The methods were applied to 46 time series comprising six aphid species from five sites and four moth species from six sites. There were few positive Lyapunov exponents and none was sufficiently large to characterize its time series as chaotic. Zhou *et al.* (1997) found that there were differences in the mean and the skewness of the randomization distributions of the Lyapunov exponent from the two hypotheses. Attempts have been made to derive confidence limits for Lyapunov exponent estimates by using replicated laboratory populations or populations from different geographic locations, and this approach might well prove a sensible way forward. However, this study showed that estimates of Lyapunov exponents may be very different at different localities, especially for species with a three-lag model. Of course, it must be stressed that these results may apply only at the spatial and temporal scales studied. Lyapunov exponent estimates were slightly greater for aphids, which have relatively complex life histories, than for moths, although it is still unclear whether the differences between life history strategies in aphids and moths are related to their strength of density-dependence (Hanski & Woiwod, 1993). Non-linearity is necessary, although not sufficient, for producing chaotic dynamics. Statistical methods have been developed to test for the non-linearity of a time series, although Zhou *et al.*'s methods to estimate Lyapunov exponents may be used independently of these.

A recent study (Costantino *et al.*, 1997) suggested that their laboratory data of the population dynamics of the flour beetle *Tribolium castaneum* showed convincing evidence of transitions to chaos. However, their methodology was similar to those earlier studies that assessed the population dynamics of a time series by fitting some mechanistic or empirical model and then inspecting realizations from the deterministic skeleton of the fitted model. The reported estimates of the Lyapunov exponents in

Costantino *et al.*'s data must be shown to be robust to the presence of the noise that they themselves estimate in their variance-covariance matrix Σ , for a valid characterization of the *Tribolium* dynamics. The next step will be for Costantino *et al.* to report such estimates for the stochastic version of their model and to compare their data with the output from this, rather than that from the deterministic skeleton. Until then, their characterization of the *Tribolium* dynamics must be viewed with caution.

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