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The irreducible uncertainty of the demography–environment interaction in ecology

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The interpretation of ecological data has been greatly improved by bridging the gap between ecological and statistical models. The major challenge is to separate competing hypotheses concerning demography, or other ecological relationships, and environmental variability (noise). In this paper we demonstrate that this may be an arduous, if not impossible, task. It is the lack of adequate ecological theory, rather than statistical sophistication, which leads to this problem. A reconstruction of underlying ecological processes can only be done if we are certain of either the demographic or the noise model, which is something that can only be achieved by an improved theory of stochastic ecological processes. Ignoring the fact that this is a real problem may mislead ecologists and result in erroneous conclusions about the relative importance of endogenous and exogenous factors in natural ecosystems. The lack of correct model identification may also have far-reaching consequences for population management and conservation.

Keywords: population dynamics; environmental noise; model uncertainty; time-series

1. INTRODUCTION

The essence of science is to describe and explain patterns in terms of the underlying processes (Levin 1992). Since the dawn of ecology, data have been collected and analysed in the hope that the true underlying biological structure of the system will thus be revealed (Elton 1924, Stenseth 1999). In order to describe and analyse data we must be guided by theory (Hilborn & Mangel 1997). It has been argued that a sound theoretical model is essential to all ecological interpretation and understanding (e.g. Berryman 1992, 1999). In practice, this means that one, or several, models of the system in question must be specified. In population ecology different model structures represent different hypotheses about the deterministic demographic structure of the population (Royama 1992; Higgins *et al.* 1997; Stenseth *et al.* 1999a,b). It is important to note that, at a more abstract level, we are actually interested in modelling the information in the data rather than the data itself (Burnham & Anderson 1998). The choice between models, given data, can be guided by different criteria, some of them with a strong information-theoretic underpinning. For example, the Akaike information criterion (AIC) provides an estimator of the relative Kullback–Leibler information—the information lost when using a model for approximating full reality—when the underlying philosophy is model selection based on the principle of parsimony (Burnham & Anderson 1998). This attempt to use putative objective criteria can, however, be modified by either prior corroborated knowledge (not incorporated in the *a priori* models) of the study system or by conflicting information from other analyses (Punt & Hilborn 1997; Burnham & Anderson 1998).

When fitting models to data, assuming no observation error, the residuals are interpreted as a so-called process error, i.e. stochasticity inherent to the process described (Hilborn & Mangel 1997). According to statistical model selection procedures, a good model should be constructed such that the residuals are (i) normally distributed, and (ii) without any obvious autocorrelation, (iii) free from outliers, and (iv) free of any apparent pattern (Chatfield 1999). In ecology, however, the process error, often denoted environmental stochasticity or noise, is believed to deviate from those assumptions, e.g. be autocorrelated and dominated by low-frequency variation (Steele 1985; Warner *et al.* 1995; Halley 1996), offering a possible explanation for the reddened spectra that characterize many ecological time-series (Lawton 1988; Pimm & Redfearn 1988).

One of the most important sources of information about demography and environmental variability is time-series data on population abundance or density. It is commonly believed that, provided that measurements are accurate and the time-series is long enough, a correct identification of the demographic structure is possible. Under certain controlled circumstances this may in fact be possible (Bjørnstad *et al.* 2001), although it is not clear how generally feasible that is. In this paper we demonstrate that reconstructing the demography is extremely difficult, misleading and often proves to be a search in vain. It is shown that this is not just a statistical problem in the usual sense (e.g. lack of sufficient data), but also a result of fundamental model uncertainty and the inverse problem (Wood 1997) of trying to understand the underlying processes from the observation of patterns.

For this purpose, we simulated a simple autoregressive (AR) model of order 2 with two parameters (a_1 and a_2). We applied common-system identification tools (Söderström & Stoica 1989; Ljung & Glad 1994) to investigate this AR(2)-skeleton modulated by a random deviate (noise).

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Hence, the true demographic structure of the system, as well as the environmental noise affecting it, was known. We chose an AR(2) time-series approach to illustrate the problem of model reconstruction for the following reasons. First, much ecological information does indeed come in the form of time-series of various lengths and precision. Second, the AR structure allowed us to highlight a common problem in ecological data interpretation, namely the fact that population time-series are often temporally, positively autocorrelated. This observation leads us directly to the general problem of separating demography from environment. Positively autocorrelated time-series have three possible explanations: (i) there are built-in time-lags in the population such that delayed density-dependent feedback generates a reddened series (Kaitala & Ranta 1996); (ii) the environmental variability is reddened, as suggested above, and the population passively mirrors that variability (Lawton 1988; Pimm & Redfearn 1988); or (iii) a combination of both.

2. MATERIAL AND METHODS

For our current purposes we used the second order autoregressive process, AR(2), modulated with a noise $\mu(t)$ as follows

$$X(t+1) = \delta + a_1 X(t) + a_2 X(t-1) + \mu(t). \quad (2.1)$$

Here a_1 and a_2 are the model parameters, δ is a constant ($\delta = 0$). The noise $\mu(t)$ modulating the AR(2) process was generated after Ripa & Lundberg (1996)

$$\mu(t) = \kappa \mu(t-1) + s \sqrt{1-\kappa^2} w(t), \quad (2.2)$$

where κ is a parameter ($-1 < \kappa < 1$) determining the degree of autocorrelation and the term $s\sqrt{1-\kappa^2}$ is the standard deviation of the random normal deviate w . The results presented here (figure 1) are for w -values ranging from -0.25 to 0.25 (but we have also experimented with a much wider range of w -values, and the results remained the same as in figure 1). The values of w were corrected such that the variance was independent of the values of κ (Ripa & Lundberg 1996). Thus, instead of a pure AR(2) dynamic the generated time-series X is a series modulated with the noise $\mu(t)$ of known autocorrelation structure. Note that even though the noise process may be far more complicated in real systems, an AR(2) process was used here to illustrate our results. We initiated the system with uniform random numbers (between 0 and 1) and let the process run for 600 time-steps. The final 100 steps were used to fit an AR(2) model to the noise-modulated time-series to obtain estimates for a_1 and a_2 . In this process we used the standard criteria of systems identification (Söderström & Stoica 1989; Ljung & Glad 1994). The procedure was repeated for all feasible parameter values of a_1 and a_2 ($a_2 + a_1 < 1$, $a_2 - a_1 < 1$, and $-1 < a_2 < 1$).

To assess the consistency of the parameter estimates we repeated the process 100 times and fitted the AR(2) model to the time-series. For our criterion of consistency, we simply scored how many times the parameter estimates for a_1 and a_2 fell within $\pm 10\%$ of the average of the 100 replicated runs. The results (not displayed here) indicated very high consistency from one independent run to another. Finally, using the partial autocorrelation technique (Chatfield 1999) we scored the order of the dynamics, X , generated by the noise-modulated AR(2) process.

3. RESULTS

The estimates of the parameters a_1 and a_2 can be very inaccurate under coloured (autocorrelated) noise (figure 1a,e). The process order is often incorrectly estimated resulting in an erroneous (compared to the true process) lag structure (figure 1). For example, coloured noise (figure 1b,f) often yields lags of order of more than 2 (the true lag). Positive lags of order 3 or 4 may seem biologically implausible, but confronted with such lags obtained from the data an explanation is still required as to whence the extra lags emanate (Royama 1992). Conversely, should the significant lags of that order be negative, then there is still a margin for misinterpreting the biological process because such high lags are certainly biologically conceivable (Gillman & Dodd 2000). Experimentation with the parameter that determines the degree of autocorrelation (colour) of the noise (κ) ranging from -0.9 to 0.9 shows that incorrectly identified lags will already have appeared when $|\kappa| > 0.2$ and also when the noise variance is very moderate. We conclude that the probability of correctly reconstructing the process order is contingent on the magnitude, as well as the autocorrelation ('colour'), of the noise (determined by κ).

Second, for a given model structure the parameter estimates are consistently very biased (figure 1a,c,e). For example, with blue noise, $\kappa = -0.9$, the estimates of a_1 are biased towards negative values, whereas the reverse is true for red noise, $\kappa = 0.9$ (figure 1a). Hence, the noise and the deterministic skeleton work in concert such that the skeleton is no longer recognizable in the resulting time-series (Ranta *et al.* 2000). Note that uncorrelated (white) noise generates no such problems, either in the identification of the process order or in the parameter estimation. The consistency of the parameter estimates is, however, also affected by white noise such that the estimates of the parameter values are more consistent for positive than for negative demographic parameter values. Our ability to achieve consistent parameter estimates will therefore, independent of the noise colour, differ between populations having a different demography (values of a_1 and a_2), potentially representing different life histories. Thus, we conclude that with coloured noise modulating the underlying dynamics, identification of process order and parameter values of the AR(2) process becomes largely futile (figure 1).

4. DISCUSSION

The problem of interpreting model parameters estimated from time-series data has previously been discussed in the ecological literature (Williams & Liebhold 1995, 1997; Berryman & Turchin 1997) and Berryman & Turchin (2001) have correctly highlighted the problems and pitfalls of time-series analysis as the sole tool for understanding population processes. We argue that this is not only a statistical problem (Royama 1981; Williams & Liebhold 1997; Williams & Liebhold 2000), but that the interplay between demography and environmental stochasticity may ruin the interpretation at a more fundamental level. For a given population, the relevant environmental noise to be taken into account is not a single abiotic factor, but rather the combined effect of all abiotic

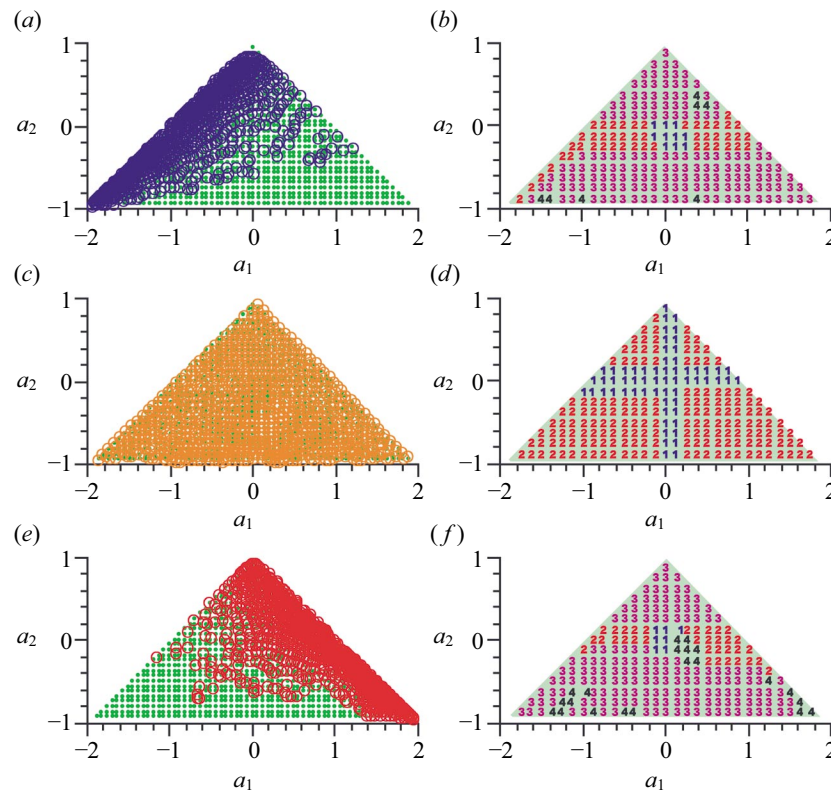


Figure 1. AR(2) parameters (a, c, e) and the process order (b, d, f) estimated from the noise-modulated dynamics. Green dots in the triangle ($a_2 + a_1 < 1$, $a_2 - a_1 < 1$, and $-1 < a_2 < 1$) are the values used to generate the time-series X affected by the external noise μ (equations (2.1) and (2.2)), while open rings (blue for $\kappa = -0.9$, orange for $\kappa = 0$, and red for $\kappa = 0.9$) indicate the values obtained by fitting an AR(2) model to the noise-modulated data. The order estimates (numbers inserted in b, d , and f) were achieved by using the partial-autocorrelation technique (Chatfield 1999).

and biotic factors affecting birth and death rates. Steele (1985) demonstrated that the long time-scales of heat transport and transfer in marine systems ensure that the environmental conditions change slowly. Hence, marine abiotic factors tend to be positively autocorrelated on an annual time basis. Whereas many abiotic factors in terrestrial systems can be safely treated as white noise, at least on time-scales of less than 50 years (Steele 1985), climatic indices, such as the North Atlantic Oscillation (NAO) (Hurrell *et al.* 2001) are often both positively autocorrelated and commonly used in ecological studies (Post *et al.* 1999). Finally, the biotic component of the process error further increases the likelihood of autocorrelated error terms in ecology simply because many populations change slowly and population density in one year tends to be positively correlated with the density of the previous year. Hence, it may not be premature to suggest that there is at least some evidence for autocorrelated feedback environments.

So, what should ecologists do? Some authors suggest that time-series analysis should be used for diagnosis rather than modelling (e.g. Berryman & Turchin 1997; Berryman 1999). The results should then be considered as clues instead of facts. We agree that diagnosis could be an important first step in an ecological investigation and our critique here is restricted to ecological modelling. However, ecologists should try to progress much further. In fact, we already go far beyond simple diagnosis when we use time-series data to parameterize models used for decision-making in fisheries management (Quinn & Deriso 1999).

The problem illustrated here, using model reconstruction from time-series data with known demographic and noise structures, is not only of theoretical interest. For example, estimates of population viability hinge on the correct identification of noise and demography (Ripa & Lundberg 1996; Halley & Iwasa 1998). However, it is not only in population dynamics, as illustrated with the example here, but in all analyses of ecological data where error terms are likely to be serially correlated, where this uncertainty becomes critical. Information from experiments or comparative studies in all natural systems generally cover many events in temporal sequence. Although not viewed as time-series data *per se*, data from such studies inevitably have to deal with the problem of disentangling demography (or ecological interactions of higher order) from 'environment'. However, to generate time-series from experiments (see, for example, Carpenter *et al.* 1996) may give more informative and detailed data and may therefore be less vulnerable to the critique presented here. In fact, experiments in aquatic microcosms allow even the environmental stochasticity to be controlled (e.g. Petchey 2000).

5. CONCLUSIONS

This paper highlights a fundamental philosophical problem with far-reaching influence on applied ecology. If no detailed prior information is available about either the deterministic skeleton or the environmental noise (as is often the case with real population data), deciding what elements should be included in the model and what

should be left in the residuals is difficult. Hence, demography and environment cannot be separated. From a strictly statistical viewpoint this is not a problem, since a good model should always be accompanied by uncorrelated, normally distributed residuals (Chatfield 1999). This reasoning ignores the fact that structured noise is often a better null model for abiotic environmental variation and that biological processes and interactions tend to modulate the noise further (Ripa *et al.* 1998). Hence, the best course is to consider multiple hypotheses about demography and environment, and—based on fundamental information-theoretic underpinning—assign each hypothesis a relative probability given the data available (Hilborn & Mangel 1997; Burnham & Anderson 1998). This approach acknowledges the authors' fundamental uncertainty about the *a priori* model. As a consequence, the interpretation of the relative importance of endogenous and exogenous factors will be uncertain, if not impossible to reveal, unless the most important factors are measured and incorporated into the estimation framework. Such a framework has been devised by several authors (Royama 1992; Berryman 1999; Berryman & Turchin 2001).

We are currently at the stage where the 'laws' (Turchin 2001) or 'principles' (Berryman 1999) of population dynamics are finally gaining some general acceptance. Furthermore, recent studies of well-controlled systems in the laboratory give inspiration and it is to be hoped that progress can, indeed, be made (Bjørnstad *et al.* 2001). The problems highlighted in this paper should not cast any shadow upon these achievements. However, it remains to be demonstrated that natural systems can be understood as easily as controlled experiments. The enigmatic fluctuations of natural populations also require such scientific understanding.

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