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A CRITICAL SMOOTHING TEST FOR MULTIPLE EQUILIBRIA

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Abstract. If a population has multiple positive stable equilibria, this information can be useful in natural-resource management. We describe a test for the presence of multiple, potentially stable equilibria in a single population. The test is based on the idea of critical smoothing. Critical smoothing was originally proposed for testing for multiple modes in a probability density function. The test is illustrated using data for the spruce budworm and the snowshoe hare.

Key words: bandwidth of a kernel estimator; bootstrap procedures for time series; critical-smoothing test; kernel estimation; multiple equilibria, test; snowshoe hare; spruce budworm.

Introduction

The possibility that plant and animal populations have multiple positive equilibria has received considerable attention in the ecological literature. Examples include fish (e.g., Peterman 1977, Spencer and Collie 1997), insects (e.g., Ludwig et al. 1978, Kuussaari et al. 1998), and phytoplankton (e.g., Beltrami 1989). Beyond its scientific interest, this possibility has implications for the conservation and management of natural systems (Carpenter 2001). This paper is concerned with the problem of testing for the existence of multiple, potentially stable positive equilibria in a single population. This problem does not appear to have been treated in the literature and the approach proposed here should be viewed as a first step.

To fix ideas, let X_t be the level or density of a population in period *t.* A general stochastic model of the dynamics of this population is

$$X_t = X_{t-1}F(X_{t-1})\exp(\varepsilon_t) \qquad (1)$$

where F is a nonnegative function and ε_t is a normal process error with mean 0 and variance σ^2. This model can be rewritten as

$$Y_t = \log(X_t/X_{t-1}) = f(X_{t-1}) + \varepsilon_t \qquad (2)$$

where $f = \log F$. This has the form of a regression model. That is, the growth function f can be estimated by the regression of observed values of Y_t against the corresponding values of X_{t-1}. A population-level $\bar{X}$ corresponding to a so-called ''0-downcrossing'' of f (i.e., $f(\bar{X}) = 0$ and $f'(\bar{X}) < 0$) is a potentially stable equilibrium of the deterministic skeleton of Eq. 1. The equilibrium notion extends to the stochastic model, in the sense that a population in the neighborhood of $\bar{X}$ tends to remain there provided σ^2 is not too large.

The problem considered in this paper is testing the null hypothesis H_0 that f has one 0-downcrossing against the alternative hypothesis H_1 that it has more than one, based on a population time series $X_1, X_2, \ldots, X_n$. We will assume that measurement error in this series is small in comparison to process error. One way to proceed would be to adopt a parametric model for f in which the number of 0-downcrossings is controlled by one or more parameters. In this way, the problem would be reduced to one of more or less standard parametric inference. As the results of this approach are sensitive to mis-specification of the parametric model for f, we will take a nonparametric approach based on the idea of critical smoothing (Silverman 1981).

The Test

The critical-smoothing test is based on estimating the growth function f in the regression model (Eq. 2) by kernel estimation. Briefly, kernel estimation is a method of nonparametric regression that estimates $f(x)$ by a weighted average of values of Y_t with the weight on Y_t inversely related to the distance $|x - X_{t-1}|$. An excellent introduction to kernel estimation is provided in the monograph by Wand and Jones (1995). The use of kernel estimation in nonlinear time-series analysis was reviewed by Hardle et al. (1997).

A crucial parameter of any kernel estimator is the bandwidth. The bandwidth controls the smoothness of

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the kernel estimate by specifying the rate at which the weights decline with distance. Let $\hat{f}(x;\ h)$ be a kernel estimate of f using bandwidth h and having the special property that the number of its 0-downcrossings is a nonincreasing function of h. A particular choice of $\hat{f}(x;\ h)$ is given below. For small values of h, $\hat{f}(x;\ h)$ will be rough and will typically have more than one 0-downcrossing. These 0-downcrossings may be due to the process error, which contributes to the variability in Y_t, or to genuine features of f. Let h_{crit} be the smallest bandwidth for which $\hat{f}(x;\ h)$ has a single 0-downcrossing. The idea underlying critical smoothing is that 0-downcrossings of $\hat{f}(x;\ h)$ arising from genuine features of f are less easily annihilated by increasing h than those arising solely from process error. This suggests that h_{crit} itself can be used as a test statistic, with H_0 rejected in favor of H_1 for large values of h_{crit}. In technical terms, the kernel estimate $\hat{f}(x;\ h_{\text{crit}})$ corresponds to the member of the family $\{\hat{f}(x;\ h)\}$ indexed by h that is closest to satisfying H_1 yet that still satisfies H_0. It is not intended as the final estimate of f. In most cases in which H_0 is not rejected, f would be estimated using a bandwidth larger than h_{crit}, while a smaller bandwidth would be used when H_0 is rejected.

It remains to assess the significance level of the observed value of h_{crit}. One possibility is to assess significance against a fitted parametric model with a single 0-downcrossing. This approach is unacceptably sensitive to mis-specification of the parametric model, so it is not recommended unless the risk of mis-specification is small. Instead, the following bootstrap procedure can be used. Let

$$R_t = Y_t - \hat{f}(X_{t-1};\ h_{\text{crit}})\quad t = 2, 3, \ldots, n \tag{3}$$

be the critical-smoothing residuals. Simulate a new population time series according to

$$X_t^* = X_{t-1}^* \exp[\hat{f}(X_{t-1}^*;\ h_{crit})]\exp(\varepsilon_t^*)\qquad t = 2, 3, \ldots, n \tag{4}$$

with $X_1^* = X_1$ and where ε_t^* is a bootstrap error sampled at random with replacement from the critical-smoothing residuals. Let h_{crit}^* be the critical bandwidth found from the simulated series (Eq. 3). Repeat the procedure a large number of times and estimate the significance level of h_{crit} by the proportion of simulated series for which $h_{\text{crit}}^* > h_{\text{crit}}$. Let $\hat{f}^*(x;\ h)$ be the kernel estimate with bandwidth h based on the simulated series. As the number of 0-downcrossings is nonincreasing in h, $h_{\text{crit}}^* > h_{\text{crit}}$ if and only if $\hat{f}^*(x;\ h_{\text{crit}})$ has multiple 0-downcrossings. Thus, to determine whether $h_{\text{crit}}^* > h_{\text{crit}}$, it is only necessary to form $\hat{f}^*(x;\ h_{\text{crit}})$ and count its 0-downcrossings.

Critical smoothing was originally proposed by Silverman (1981) for inference about the number of modes in a probability density function—see, also, Harezlak and Heckman (2001). It was applied in this context to ecological data by Manly (1996) to investigate multimodality in size distributions. In an application closer to ours, Bowman et al. (1998) used critical smoothing to test monotonicity of a regression function. Bootstrap methods for time-series data are reviewed in Berkowitz and Kilian (2000).

Two problems arise in selecting a kernel estimator to use in this procedure. The first is that the number of 0-downcrossings must be nonincreasing in the bandwidth h. The second is that, as a consequence of the multiplicative process error in (Eq. 1), the observations in the regression (Eq. 2) will typically be denser at small values of X_{t-1} than at large values. To address these problems, we will use the following kernel estimator:

$$\hat{f}(x;\ h) = \sum_{t=2}^{n} Y_t \left\{\Phi\left[\frac{U(t) - \log x}{h}\right] - \Phi\left[\frac{L(t) - \log x}{h}\right]\right\} \tag{5}$$

where Φ is the standard normal distribution function and where

$$L(t) = \begin{cases} -\infty & t = 2 \\ (\log X_{t-2} + \log X_{t-1})/2 & t > 2 \end{cases} \tag{6}$$

and

$$U(t) = \begin{cases} \infty & t = n \\ \log X_{t-1} + \log X_t)/2 & t < n. \end{cases} \tag{7}$$

This corresponds to the Gasser-Muller kernel estimator (Gasser and Muller 1979) with a Gaussian kernel and a log transformation of the regressor variable. Chaudhuri and Marron (2000) showed that the number of 0-downcrossings of the Gasser-Muller estimate with a Gaussian kernel is nondecreasing in h. The logarithmic transformation of the regressor ensures a more uniform distribution of regressor values (Hart 1997).

Application to Simulated Data

In this section, the critical-smoothing test is applied to data simulated from the following model:

$$X_t = [X_{t-1} + rX_{t-1}(1 - X_{t-1}/K) - X_{t-1}^2/(1 + X_{t-1}^2)]\exp(\varepsilon_t). \tag{8}$$

This is the stochastic version of the discrete-time homologue to the reduced-form, continuous-time model proposed by Ludwig et al. (1978) for outbreaks of the spruce budworm *Choristoneura fumiferana*. An actual population time series for this species is analyzed in the following section. Here, the values of n, K, and σ are fixed at 50, 10, and 0.2, respectively, and two values of the parameter r—0.75 and 0.5—are considered. In Fig. 1, the corresponding growth functions are plotted. For $r = 0.75$, this function has a single 0-downcrossing at $x = 8.4$, while for $r = 0.5$, it has 0-downcrossings at $x = 0.63$ and 7.3 separated by a 0-upcrossing at $x = 2.0$.

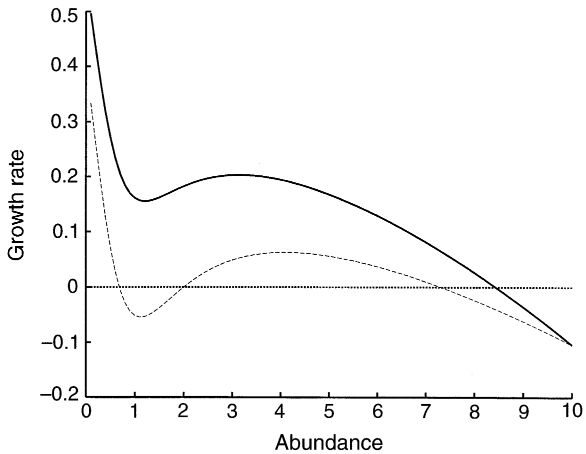

FIG. 1. Growth functions $f(X_{t-1})$ used in the simulation experiment (r = 0.75, solid line; r = 0.5, dashed line). See *Application to simulated data* for details.

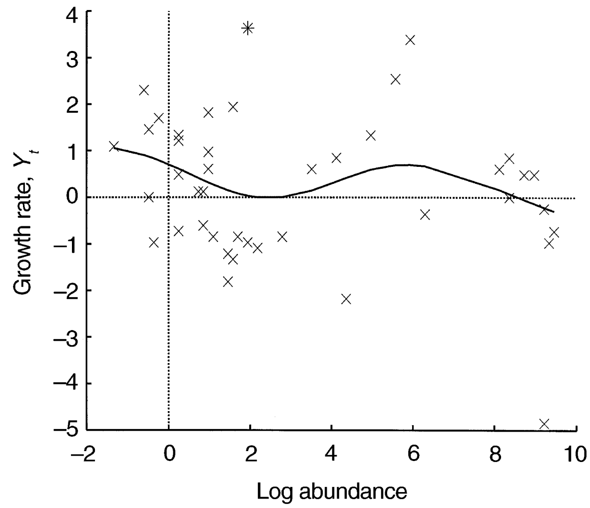

FIG. 3. Growth rate (Y_t) plotted against log abundance ($\log X_{t-1}$) for the spruce budworm data in Fig. 2. Also shown is the kernel estimate using the critical bandwidth 1.73. The outlying observation indicated by "⁎" was omitted from the analysis.

For each value of r, a total of 100 series were simulated from Eq. 8 with initial value $X_1 = 8.4$ when $r = 0.75$ and $X_1 = 2.0$ when $r = 0.5$ (Appendix A). The critical-smoothing test was applied at the nominal 0.10 significance level based on 100 bootstrap series. For $r = 0.75$, the null hypothesis of a single 0-downcrossing was incorrectly rejected for 9 of 100 simulated series for an estimated significance level of 0.09 with 1 SE $\approx$ 0.03. This is not significantly different from the nominal level of 0.10. For $r = 0.5$, the null hypothesis was correctly rejected for 22 of 100 simulated series for an estimated power of only 0.22 with 1 SE $\approx$ 0.04. This low power is explained by the fact that not all of the simulated series actually visited the neighborhoods of both steady states. This problem is not confined to the critical-smoothing test: it is hard to imagine any test that can detect the presence of a steady state in a time series that does not visit its neighborhood. The experiment was repeated retaining only simulations with at least five observations below the lower steady state and at least five observations above the upper steady state. In this case, the null hypothesis was correctly rejected for 89 of 100 simulations for an estimated power of 0.89 with 1 SE of around 0.04.

APPLICATION TO REAL DATA

In this section the critical-smoothing test is applied to two real population time series. The first is an annual time series of the larval density of the spruce budworm *Choristoneura fumiferana* near Chapleau in Quebec, Canada, over the 46-year period 1930–1975 (see Appendix B). The time series of log densities, which was

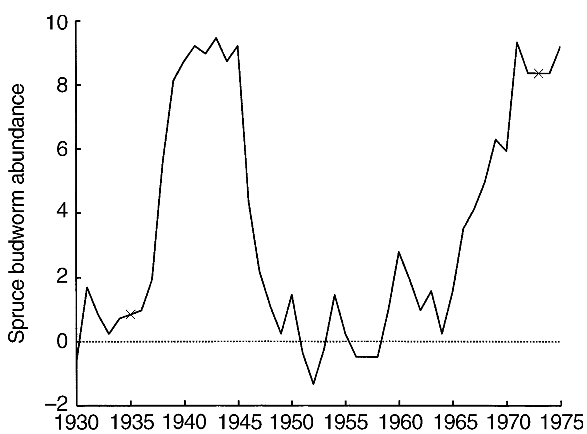

FIG. 2. Annual time series of log larval abundance of the spruce budworm near Chapleau (Quebec, Canada) 1930–1975 (after Royama 1992). Abundance is measured in number of larvae per tree. Two interpolated values are indicated by $\times$'s.

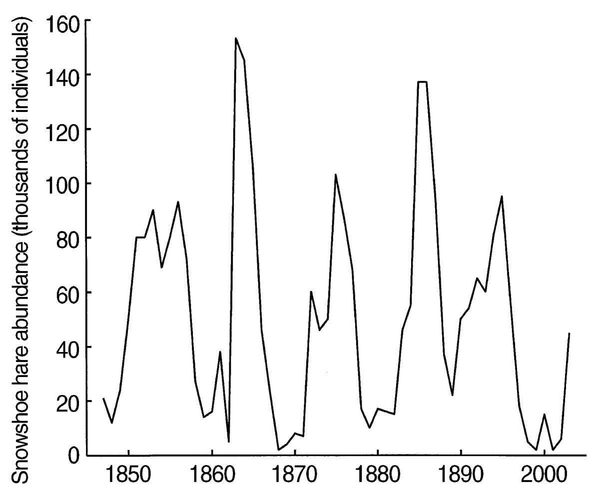

FIG. 4. Annual time series of abundance of snowshoe hare, 1847–1903 (after MacLulich 1937).

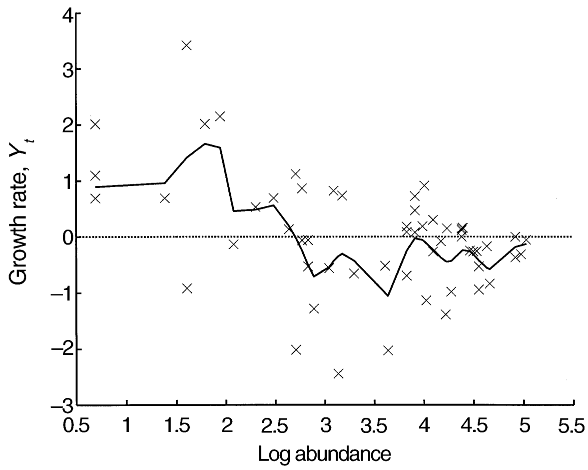

FIG. 5. Growth rate (Y_t) plotted against log abundance ($\log X_{t-1}$) for the snowshoe hare data in Fig 4.

constructed from Fig. 9.2 of Royama (1992), is shown in Fig. 2. Two missing values have been estimated by two-point linear interpolation. These interpolated values are indicated in Fig. 2. In Fig. 3, Y_t is plotted against $\log X_{t-1}$. The critical bandwidth is 1.51 and the corresponding kernel estimate is also shown in Fig. 3. Of 100 bootstrap series generated from the fitted model, h^*_{crit} exceeded 1.51 in 18 cases for an estimated significance level of 0.18 with 1 SE of around 0.04. It is clear from Fig. 3 that the single indicated outlying observation acts to mask a possible 0-downcrossing near $\log X_{t-1} = 2$. If this observation is omitted from the analysis, the critical bandwidth increases to 1.73 and the significance level estimated from 100 bootstrap series falls to 0.09 with 1 SE of around 0.03. This is at least marginally significant.

The spruce budworm is the classic example of a population exhibiting two equilibria. For contrast, we also applied the test to a population time series of the snowshoe hare *Lepus americanus* (see Appendix C). This time series, shown in Fig. 4, was compiled by MacLulich (1937) and covers the 57-year period 1847–1903. The data used here were extracted from the excellent Global Population Dynamics Database constructed and maintained by the Natural Environment Research Council's Centre for Population Biology at Imperial College's Silwood Park Campus, Berkshire, UK.[5] In Fig. 5, Y_t is plotted against $\log X_{t-1}$ for this population. In this case, the critical bandwidth h_{crit} is 0.09 and the corresponding kernel estimate is also shown in Fig. 5. Of 100 bootstrap series, h^*_{crit} exceeded 0.09 a total of 89 times for an estimated significance level of 0.89 with 1 SE around 0.04. In this case, the null hypothesis of a single 0-downcrossing cannot be rejected. Fig. 5 underscores the point that $\hat{f}(x; h_{crit})$ is not intended to be the final estimate of f, but is used only in testing H_0 against H_1. In this case, the final kernel estimate of f would use a bandwidth larger than 0.09.

[5] URL: ⟨http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html⟩

DISCUSSION

The purpose of this paper has been to take a first step in the development of nonparametric statistical tests for multiple equilibria in a single population. Although further investigation is needed, the applications to simulated and real data presented here suggest that the approach is not without promise. (See the *Supplement* for source code to perform the critical smoothing test.) The dynamics of both the spruce budworm and snowshoe hare populations almost certainly reflect interactions within webs of interacting populations. It is an open question whether, in such a situation, there is value in analyzing a single population. Of course, this question extends beyond testing for multiple equilibria to a whole range of single-population analyses. In principle, the critical-smoothing test described here can be applied to the vector version of Eq. 2. However, as a result of the so-called ''curse of dimensionality,'' the data requirements with even two interacting populations are likely to press the limit of what is available for natural systems.

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APPENDIX A

Simulated population time series of the spruce budworm (*Choristoneura fumiferana*) is available in ESA's Electronic Data Archive: *Ecological Archives* E084-037-A1.

APPENDIX B

Annual time series of larval density of the spruce budworm population near Chapleau (Quebec, Canada) during 1930–1975 is available in ESA's Electronic Data Archive: *Ecological Archives* E084-037-A2.

APPENDIX C

Population time series of the snowshoe hare (*Lepus americanus*) covering the period 1847–1903 is available in ESA's Electronic Data Archive: *Ecological Archives* E084-037-A3.

SUPPLEMENT

Source code (FORTRAN) to perform the critical smoothing test for multiple equilibria is available in ESA's Electronic Data Archive: *Ecological Archives* E084-037-S1.