

On the estimation of spread rate for a biological population

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Abstract

We propose a nonparametric estimator for the rate of spread of an introduced population. We prove that the limit distribution of the estimator is normal or stable, depending on the behavior of the moment generating function. We show that resampling methods can also be used to approximate the distribution of the estimators. © 2001 Elsevier Science B.V. All rights reserved

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1. Introduction and results

Ecologists use dispersal kernels to estimate the speed at which an introduced population might invade new environments. A kernel is fitted to the scatter of offspring locations about a parent, and this kernel is then used to calculate a velocity of spread. There is growing awareness that these estimates can be extremely sensitive to assumptions about kernel shape (Kot et al., 1996; Clark, 1998); differences in model forms that appear subtle (and fit data sets equally well), may imply large differences in velocity estimates.

We demonstrate a method that sidesteps entirely assumptions concerning kernel shape by advancing directly from empirical dispersal data to an estimator for spread rate.

A classical model for biological invasions is the integrodifference equation

$$u_{s+1}(x) = \int_{-\infty}^{\infty} R_0 G(u_s(x-y)) dF(y), \quad s = 0, 1, \dots,$$

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where $u_s(x)$ is the density of invading organisms at location $x \in R$ and time s , $R_0 > 1$ is the geometric growth rate of the population, $G(u)$ describes nonlinear growth dynamics, and F is the distribution function of a random variable X describing the distance an individual disperses in one time step. Here it is assumed that $R_0 G(u)$ has fixed points at $u = 0$ and $u = 1$, $R_0 G(u) > u$ for $0 < u < 1$, $G'(0) = 1$ and $\sup_{0 < u \leq 1} G(u)/u = 1$. Thus, the maximum per capita geometric growth is R_0 which occurs as the population density approaches 0 (Weinberger, 1982). The asymptotic spread rate of the solutions arising from compact initial data can be calculated under the assumption that the moment generating function of X

$$M(t) = \int_{-\infty}^{\infty} e^{tx} dF(x)$$

exists on some nonzero interval $[0, t_0)$. Weinberger (1982) showed that under a wide variety of assumptions on reproduction and dispersal, the rate of spread of a locally introduced population asymptotically approaches

$$c_0 = \inf_{s > 0} Z(s)$$

as the time since the initial release becomes large. Here

$$Z(t) = \frac{1}{t} \log(R_0 M(t)), \quad 0 < t < t_0.$$

The function $Z(t)$ is continuous and can be shown to have a unique critical point τ which gives a global minimum for $Z(t)$ and thus $Z'(\tau) = 0$ and

$$c_0 = Z(\tau). \quad (1.1)$$

This was proved by Weinberger (1978) for density functions $f = F'$ with bounded support (see Lemma 4.1 in Weinberger (1978) and its proof) and a straightforward extension of the proof includes the general case above (cf. Lemma 9.1 in Weinberger, 1982).

Biological measurements of dispersal distances may be available without the knowledge of the underlying distribution function. We consider how to estimate c_0 in this case. We assume that the observations X_1, X_2, \dots, X_n are independent, identically distributed random variables with distribution function F . Since we cannot assume any parametric form for F (cf. the empirical example in Kot et al. (1996)) we use a nonparametric approach. We consider the estimation of $M(t)$ with the empirical moment generating function

$$M_n(t) = \frac{1}{n} \sum_{1 \leq i \leq n} \exp(tX_i), \quad 0 \leq t < \infty.$$

This suggests that

$$Z_n(t) = \frac{1}{t} \log(R_0 M_n(t)), \quad 0 < t < \infty$$

can be used as a nonparametric estimator for $Z(t)$ and thus,

$$\hat{c}_n = Z_n(\hat{\tau}_n)$$

can be used as a nonparametric estimator for c_0 , where

$$Z'_n(\hat{\tau}_n) = 0.$$

We wish to note that the estimation of τ and c_0 fits into the general scheme of estimation based on Laplace transforms. Csörgő and Teugels (1990) introduced and investigated estimation of parameters using empirical Laplace transforms and used the general scheme in five different scenarios.

Let $t_0 = \sup\{t > 0: M(t) < \infty\} \leq \infty$ and assume throughout that $t_0 > 0$. Our first result is the strong consistency of $\hat{\tau}_n$ and \hat{c}_n .

(1.6) will be false. In the next theorem we consider the case when $t_0/2 < \tau < t_0$. Let ξ_α , $1 < \alpha < 2$ be a stable random variable with index α . We say that the random variable Y is the domain of attraction of ξ_α , if

$$\sum_{1 \leq i \leq n} (Y_i - EY_i)/(n^{1/\alpha}L(n)) \xrightarrow{\mathcal{L}} \xi_\alpha$$

with some slowly varying function L , where Y_1, Y_2, \dots, Y_n are independent copies of Y . For the properties of slowly varying functions we refer to Bingham et al. (1987).

Theorem 1.3. *If (1.3) holds and $X \exp(\tau X)$ is in the domain of attraction of ξ_α with some $1 < \alpha < 2$, then there is a slowly varying function $L_1(n)$ such that*

$$n^{1-1/\alpha}L_1(n)(\hat{\tau}_n - \tau) \xrightarrow{\mathcal{L}} \xi_\alpha. \quad (1.9)$$

If (1.1) also holds, then there is a slowly varying function $L_2(n)$ such that

$$n^{1-1/\alpha}L_2(n)(\hat{c}_n - c_0) \xrightarrow{\mathcal{L}} \xi_\alpha. \quad (1.10)$$

We note that if $X \exp(\tau X)$ is in the domain of attraction of ξ_α , then $M(\tau\alpha - \varepsilon) < \infty$ and $M(\tau\alpha + \varepsilon) = \infty$ for all $0 < \varepsilon < \tau\alpha$.

2. Bootstrap

If we wish to use (1.8) to construct confidence intervals or for hypothesis testing we need the value of the asymptotic variance v^2 . Since v^2 is unknown we must estimate it from the random sample. If v_n satisfies

$$|v_n - v| = o_p(1), \quad (2.1)$$

then under the conditions of Theorem 1.2 we have that

$$\frac{n^{1/2}(\hat{c}_n - c_0)}{v_n} \xrightarrow{\mathcal{L}} N(0, 1). \quad (2.2)$$

In the proof of (1.8) we show that

$$n^{1/2}(\hat{c}_n - c_0) = b_0(\tau)n^{1/2}(M_n(\tau) - M(\tau)) + b_1(\tau)n^{1/2}(M'_n(\tau) - M'(\tau)) + o_p(1),$$

where $b_0(\tau)$ and $b_1(\tau)$ are easily computable functions of $M(\tau)$, $M'(\tau)$ and $M''(\tau)$, say $b_0(\tau) = b_0(M(\tau), M'(\tau), M''(\tau))$ and $b_1(\tau) = b_1(M(\tau), M'(\tau), M''(\tau))$. Hence,

$$v^2 = b_0^2(\tau)(M(2\tau) - M^2(\tau)) + b_1^2(\tau)(EX^2 \exp(2\tau X) - (M'(\tau))^2) \\ + 2b_0(\tau)b_1(\tau)\{EX \exp(2\tau X) - M(\tau)M'(\tau)\}$$

and therefore the “plug in” method (i.e. replacing all expected values by the corresponding averages) gives

$$v_n^2 = \hat{b}_0^2 \{M_n(2\hat{\tau}_n) - M_n^2(\hat{\tau}_n)\} + \hat{b}_1^2 \left\{ \frac{1}{n} \sum_{1 \leq i \leq n} X_i^2 \exp(2\hat{\tau}_n X_i) - (M'_n(\hat{\tau}_n))^2 \right\} \\ + 2\hat{b}_0\hat{b}_1 \left\{ \frac{1}{n} \sum_{1 \leq i \leq n} X_i \exp(2\hat{\tau}_n X_i) - M_n(\hat{\tau}_n)M'_n(\hat{\tau}_n) \right\}, \quad (2.3)$$

where $\hat{b}_0 = b_0(M_n(\hat{\tau}_n), M'_n(\hat{\tau}_n), M''_n(\hat{\tau}_n))$ and $\hat{b}_1 = b_1(M_n(\hat{\tau}_n), M'_n(\hat{\tau}_n), M''_n(\hat{\tau}_n))$. It is easy to see that v_n of (2.3) satisfies (2.1).

Lemma 3.1. For any $0 < T < t_0$ we have

$$\sup_{0 \leq t \leq T} |M_n(t) - M(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.1)$$

$$\sup_{0 \leq t \leq T} |M'_n(t) - M'(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.2)$$

$$\sup_{0 \leq t \leq T} |M''_n(t) - M''(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.3)$$

Proof. Let

$$M_n^{(1)}(t) = \frac{1}{n} \sum_{1 \leq i \leq n} \exp(tX_i) I\{X_i \geq 0\},$$

$$M_n^{(2)}(t) = \frac{1}{n} \sum_{1 \leq i \leq n} \exp(tX_i) I\{X_i < 0\},$$

$$M^{(1)}(t) = EM_n^{(1)}(t) = \int_0^{\infty} e^{tx} dF(x)$$

and

$$M^{(2)}(t) = EM_n^{(2)}(t) = \int_{-\infty}^0 e^{tx} dF(x).$$

Proposition 1 of Csörgő and Teugels (1990) (cf. also Csörgő, 1980) yields that

$$\sup_{0 \leq t \leq T} |M_n^{(1)}(t) - M^{(1)}(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.4)$$

and

$$\sup_{0 \leq t \leq T} |M_n^{(2)}(t) - M^{(2)}(t)| \rightarrow 0 \quad \text{a.s.}$$

which give (3.1). Similarly to (3.4), Proposition 1 of Csörgő and Teugels (1990) gives the strong uniform convergence of all derivatives of $M_n^{(1)}(t)$ and $M_n^{(2)}(t)$ and, therefore, (3.2) and (3.3) are also proven. \square

Proof of Theorem 1.1. We have that

$$Z'_n(t) = -\frac{\log(R_0 M_n(t))}{t^2} + \frac{M'_n(t)}{t M_n(t)}.$$

Since

$$\lim_{t \downarrow 0} M_n(t) = 1 \quad \text{and} \quad \lim_{t \downarrow 0} M'_n(t) = \frac{1}{n} \sum_{1 \leq i \leq n} X_i,$$

we get that

$$\lim_{t \downarrow 0} Z'_n(t) = -\infty.$$

By Lemma 3.1 we have that

$$\sup_{0 \leq t \leq \varepsilon} \frac{M'_n(t)}{M_n(t)} \rightarrow \sup_{0 \leq t \leq \varepsilon} \frac{M'(t)}{M(t)} \quad \text{a.s.} \quad (3.5)$$

Lemma 3.2. We have that

$$\left| Z_n(t) - Z(t) - \frac{1}{n} \sum_{1 \leq i \leq n} \zeta_i(t) \right| = O_p(1)(M_n(t) - M(t))^2 \quad (3.9)$$

and

$$\left| Z'_n(t) - Z'(t) - \frac{1}{n} \sum_{1 \leq i \leq n} \eta_i(t) \right| = O_p(1)(M_n(t) - M(t))^2 + O_p(1)(M'_n(t) - M'(t))^2 \quad (3.10)$$

for any $0 < t < t_0$, where

$$\zeta_i(t) = c_1(t)(\exp(tX_i) - M(t))$$

and

$$\eta_i(t) = c_1(t)(X_i \exp(tX_i) - M'(t)) + c_2(t)(\exp(tX_i) - M(t)).$$

Proof. The mean-value theorem gives

$$\begin{aligned} Z_n(t) - Z(t) &= \frac{1}{t} \{ \log M_n(t) - \log M(t) \} \\ &= \frac{1}{tM(t)} (M_n(t) - M(t)) - \frac{1}{t\mu^2} (M_n(t) - M(t))^2, \end{aligned}$$

where μ is a point between $M_n(t)$ and $M(t)$. Now (3.9) follows from Lemma 3.1 with the choice of $c(t) = 1/(tM(t))$.

Similar arguments give (3.10). The details are omitted.

Lemma 3.3. If (1.1) holds, then

$$|\hat{\tau}_n - \tau - (Z'(\tau) - Z'_n(\tau))/Z''(\tau)| = o_p(1)|Z'_n(\tau) - Z'(\tau)| \quad (3.11)$$

and

$$|\hat{c}_n - c - \{Z_n(\tau) - Z(\tau) - Z'(\tau)(Z'_n(\tau) - Z'(\tau))/Z''(\tau)\}| = o_p(1)|Z'_n(\tau) - Z'(\tau)|. \quad (3.12)$$

Proof. Similarly to (3.7) we have

$$\sup_{\varepsilon \leq t \leq T} |Z''_n(t) - Z''(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.13)$$

for any $0 < \varepsilon < T < t_0/2$. The mean value theorem gives

$$Z'_n(\hat{\tau}_n) - Z'_n(\tau) = Z''_n(\xi)(\hat{\tau}_n - \tau),$$

where ξ is between $\hat{\tau}_n$ and τ . By definition $Z'_n(\hat{\tau}_n) = 0$, $Z'(\tau) = 0$ and, therefore,

$$\hat{\tau}_n - \tau = -\frac{Z'_n(\tau)}{Z''_n(\xi)} = -\frac{Z'_n(\tau) - Z'(\tau)}{Z''_n(\xi)}.$$

Hence, (3.11) follows from (3.13).

Next, we write

$$\begin{aligned} \hat{c}_n - c_0 &= Z_n(\hat{\tau}_n) - Z(\tau) \\ &= Z_n(\hat{\tau}_n) - Z_n(\tau) + Z_n(\tau) - Z(\tau) \\ &= Z'_n(\xi)(\hat{\tau}_n - \tau) + Z_n(\tau) - Z(\tau), \end{aligned}$$

where ξ is between $\hat{\tau}_n$ and τ . Using (3.7) and (3.11) we obtain immediately (3.12). \square

Using again Theorem 7.7 in Durrett (1991) we can find a slowly varying function $K^*(n)$ such that

$$n^{-1/\alpha} K^*(n) \sum_{1 \leq i \leq n} \{\exp(\tau X_i) - M(\tau)\} \xrightarrow{\mathcal{L}} \xi_\tau.$$

Comparing the tails in (3.17) and (3.18) we get from (3.18) that

$$\lim_{n \rightarrow \infty} K(n)/K^*(n) = 0$$

and therefore the proof of (3.16) is complete. \square

Proof of Theorem 2.1. Since we can follow the proof of Theorem 1.2 very closely we just give an outline. Elementary arguments similar to those proving Lemma 3.1 give that conditionally on X_n

$$\sup_{0 \leq t \leq T} |M_{m,n}(t) - M_n(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.19)$$

$$\sup_{0 \leq t \leq T} |M'_{m,n}(t) - M'_n(t)| \rightarrow 0 \quad \text{a.s.} \quad (3.20)$$

and

$$\sup_{0 \leq t \leq T} |M''_{m,n}(t) - M''_n(t)| \rightarrow 0 \quad \text{a.s.}$$

as $\min(m, n) \rightarrow \infty$. The consistency of $\hat{\tau}_{m,n}$ and $\hat{c}_{m,n}$ can be derived from (3.19) and (3.20) along the lines of the proof of Theorem 1.1. Using analogues of Lemmas 3.2 and 3.3 what we need is a central limit theorem (conditionally) for sums in the form of

$$m^{1/2} \left\{ \frac{1}{m} \sum_{1 \leq i \leq n} (b_0 \exp(\tau X_i^*) + b_1 X_i^* \exp(\tau X_i^*)) - \frac{1}{n} \sum_{1 \leq i \leq n} (b_0 \exp(\tau X_i) + b_1 X_i \exp(\tau X_i)) \right\}.$$

Since $EX^2 \exp(2\tau X) < \infty$, the required central limit theorem follows from Bickel and Freedman (1981).

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