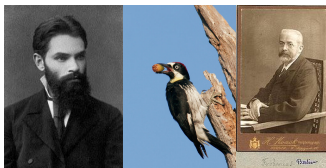


Go forth and multiply?

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June, 2012



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U.C. Davis
- Arnab Sen
Pure Mathematics and Mathematical Statistics
Cambridge

Stochastic population growth
in spatially heterogeneous environments.

Online First in *J. Math. Biol.*

Introduction

- Environmental conditions vary in space and time.
- Survivorship and fecundity depend on these conditions.
- Individuals modulate fitness by dispersing.

How does dispersal interact with environmental heterogeneity to influence population persistence?

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A mathematical “curiosity” we all know

- $Z_t :=$ population size in year t
- $f_t :=$ per-capita fitness in year t – assume i.i.d.
- $Z_{t+1} = f_t Z_t$
- $\frac{1}{t} \log Z_t$ converges a.s. to $\mathbb{E}[\log f_1] < \log \mathbb{E}[f_1]$

“Even though the expectation of population size may grow infinitely large with time, the probability of extinction may approach unity, owing to the difference between the geometric and arithmetic mean.” – Lewontin & Cohen (1969)

Continuous time analogue is the stochastic differential equation $dZ_t = \mu Z_t dt + \sigma Z_t dB_t$, where B is a one-dimensional Brownian motion: $\frac{1}{t} \log \mathbb{E}[Z_t] \rightarrow \mu$, but $\frac{1}{t} \log Z_t \rightarrow \mu - \frac{\sigma^2}{2} < \mu$.

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Of eggs and baskets

- What happens if offspring can disperse geographically throughout a set of locations where the temporal variations in fitness aren't perfectly correlated?
- That is, what happens if good years in a given region don't necessarily correspond to good years everywhere?
- In particular, are there situations where every local population would become extinct if there was no dispersal, BUT all local populations persist if there is suitable dispersal???
- YES!!!

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A continuous time model for patch fitnesses

Assume:

- n distinct patches
- $F_t^i :=$ cumulative per-capita fitness in the i -th patch at time t ,
 $\Delta F_t^i := F_{t+\Delta t}^i - F_t^i$
- $\mathbb{E}[\Delta F_t^i] \approx \mu_i \Delta t$
- $\text{Cov}[\Delta F_t^i, \Delta F_t^j] \approx \sigma_{ij} \Delta t$
- ΔF_t^i independent of past

Conclude: for B a standard n -dimensional Brownian motion,

$$dF_t^i = \mu_i dt + \sum_{j=1}^n \gamma_{ji} dB_t^j, \quad \Gamma^\top \Gamma = \Sigma \quad (\top \text{ means transpose})$$

$$d\mathbf{F}_t = \boldsymbol{\mu} dt + \Gamma^\top d\mathbf{B}_t \quad (\text{column vectors!})$$

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Incorporating dispersal into the continuous time model

- $D_{ji} :=$ the **per-capita rate** at which the population in patch j **disperses** to patch i , $j \neq i$
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Suitable data can be collected

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ESTIMATION OF GROWTH AND EXTINCTION PARAMETERS FOR ENDANGERED SPECIES¹

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Moscow, Idaho 83843 USA

Abstract. Survival or extinction of an endangered species is inherently stochastic. We develop statistical methods for estimating quantities related to growth rates and extinction probabilities from time series data on the abundance of a single population. The statistical methods are based on a stochastic model of exponential growth arising from the biological theory of age- or stage-structured populations. The model incorporates the so-called environmental type of stochastic fluctuations and yields a lognormal probability distribution of population abundance. Calculation of maximum likelihood estimates of the two unknown parameters in this model reduces to performing a simple linear regression. We describe techniques for rigorously testing and evaluating whether the model fits a given data set. Various growth- and extinction-related quantities are functions of the two parameters, including the continuous rate of increase, the finite rate of increase, the geometric finite rate of increase, the probability of reaching a lower threshold population size, the mean, median, and most likely time of attaining the threshold, and the projected population size. Maximum likelihood estimates and minimum variance unbiased estimates of these quantities are described in detail.

We provide example analyses of data on the Whooping Crane (*Grus americana*), grizzly bear (*Ursus arctos horribilis*) in Yellowstone, Kirtland's Warbler (*Dendroica kirtlandii*), California Condor (*Gymnogyps californianus*), Puerto Rican Parrot (*Amazona vittata*), Palila (*Loxioides bailleui*), and Laysan Finch (*Telespiza cantans*). The model results indicate a favorable outlook for the Whooping Crane, but long-term unfavorable prospects for the Yellowstone grizzly bear population and for Kirtland's Warbler. Results for the California Condor, in a retrospective analysis, indicate a virtual emergency existed in 1980. The analyses suggest that the Puerto Rican Parrot faces little risk of extinction from ordinary environmental fluctuations, provided intensive management efforts continue. However, the model does not account for the possibility of freak catastrophic events (hurricanes, fires, etc.), which are likely the most severe source of risk to the Puerto Rican Parrot, as shown by the recent decimation of this population by Hurricane Hugo. Model parameter estimates for the Palila and the Laysan Finch have wide uncertainty due to the extreme fluctuations in the population sizes of these species. In general, the model fits the example data sets well. We conclude that the model, and the associated statistical methods, can be useful for investigating various scientific and management questions concerning species preservation.

Key words: California Condor; conservation biology; diffusion process; endangered species; exponential growth; extinction; grizzly bear; inverse Gaussian distribution; Kirtland's Warbler; Laysan Finch; lognormal distribution; Palila; parameter estimation; Puerto Rican Parrot; stochastic differential equation; stochastic population model; Whooping Crane; Wiener process.

A random matrix connection

- Recall

$$d\mathbf{X}_t = \left(\mu \diamond \mathbf{X}_t + D^\top \mathbf{X}_t \right) dt + \mathbf{X}_t \diamond \Gamma^\top d\mathbf{B}_t.$$

- Note that

$$\mathbf{X}_k = M_k \cdots M_1 \mathbf{X}_0,$$

where the M_ℓ are i.i.d. random matrices.

- Consequently, if $S_t := X_t^1 + \cdots + X_t^n =$ total population size at time t , then

$$\chi := \lim_{t \rightarrow \infty} t^{-1} \log S_t$$

exists a.s. (Kingman subadditive ergodic theorem, Oseledets multiplicative ergodic theorem, Furstenberg–Kifer,...).

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Patch proportions

- Set $\mathbf{Y}_t := (Y_t^1, \dots, Y_t^n)^\top$, where $Y_t^j := X_t^j / (X_t^1 + \dots + X_t^n)$ is the **proportion of individuals in patch j** .
- By Itô, \mathbf{Y} satisfies the **autonomous SDE**

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- If D is **irreducible** and $\boldsymbol{\Sigma}$ has **full rank**, then there is a **random variable \mathbf{Y}_∞** on the **probability simplex** $\{\mathbf{y} \in \mathbb{R}^n : \sum_i y_i = 1, y_i \geq 0\}$ such that for any initial conditions $\frac{1}{t} \int_0^t \delta \mathbf{Y}_s ds$ converges almost surely to the law of \mathbf{Y}_∞ . Averaged over time, the proportion of the population in each patch stabilizes to a random (patch-dependent) limit.

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- If D is **irreducible** and Σ has **full rank**, then there is a **random variable \mathbf{Y}_∞** on the **probability simplex** $\{\mathbf{y} \in \mathbb{R}^n : \sum_i y_i = 1, y_i \geq 0\}$ such that for any initial conditions $\frac{1}{t} \int_0^t \delta \mathbf{Y}_s ds$ converges almost surely to the law of \mathbf{Y}_∞ . **Averaged over time, the proportion of the population in each patch stabilizes to a random (patch-dependent) limit.**

Total population size

- Recall that $S_t := X_t^1 + \dots + X_t^n =$ **total population size at time t** .
- Note

$$\begin{aligned} dS_t &= \mu^\top \mathbf{X}_t dt + \mathbf{X}_t^\top \Gamma^\top d\mathbf{B}_t \\ &= S_t \mu^\top \mathbf{Y}_t dt + S_t \mathbf{Y}_t^\top \Gamma^\top d\mathbf{B}_t. \end{aligned}$$

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$$\begin{aligned} \log S_t &= \log S_0 + \int_0^t \mathbf{Y}_s^\top \Gamma^\top d\mathbf{B}_s \\ &\quad + \int_0^t \mu^\top \mathbf{Y}_s ds - \frac{1}{2} \int_0^t \mathbf{Y}_s^\top \Sigma \mathbf{Y}_s ds. \end{aligned}$$

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Exponential growth – the Lyapunov exponent

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Two uncorrelated patches ($n = 2$)

- Assume there are two patches (i.e. $n = 2$) and, for simplicity, that $\sigma_{ii} = \sigma_i^2$ and $\sigma_{ij} = 0$ for $i \neq j$.
- The limit $Y_\infty = (Y_\infty^1, Y_\infty^2) = (Y_\infty^1, 1 - Y_\infty^1)$ is such that Y_∞^1 has density

$$\rho(y) = Cy^{\beta-\alpha_1}(1-y)^{-\beta-\alpha_2} \exp\left(-\frac{2}{\sigma_1^2 + \sigma_2^2} \left(\frac{D_{21}}{y} + \frac{D_{12}}{1-y}\right)\right),$$

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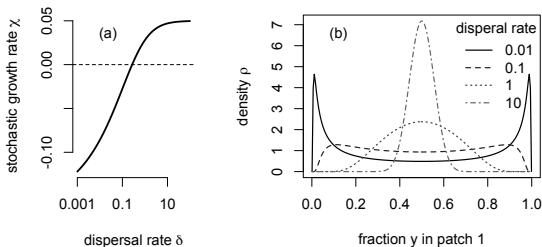
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Two uncorrelated patches with identical characteristics



Population growth and spatial distribution in a two patch environment. Parameter values are $\mu_1 = \mu_2 = 0.3$, $\sigma_1^2 = \sigma_2^2 = 1$, and $D_{12} = D_{21} = \delta$. In (a), the stochastic growth rate χ plotted as a function of the dispersal rate δ . In (b), the stationary density of the fraction of individuals in patch 1. Increasing the dispersal rate pushes the system from extinction to persistence.

Ideal free dispersal

- Suppose the **environmental conditions** μ and Σ are **fixed**.
- What form of dispersal (i.e. choice of D) maximizes χ ?
- Recall that $\chi = \mu^\top \mathbb{E}[\mathbf{Y}_\infty] - \frac{1}{2} \mathbb{E}[\mathbf{Y}_\infty^\top \Sigma \mathbf{Y}_\infty]$. Jensen's inequality gives

$$\mathbb{E}[\mathbf{Y}_\infty^\top \Sigma \mathbf{Y}_\infty] \geq \mathbb{E}[\mathbf{Y}_\infty]^\top \Sigma \mathbb{E}[\mathbf{Y}_\infty].$$

- We want $\mathbf{Y}_\infty = \pi$ for some constant vector π maximizing

$$\mu^\top \pi - \frac{1}{2} \pi^\top \Sigma \pi$$

subject to the constraints $\sum_i \pi_i = 1$ and $\pi \geq 0$.

- Maximum “achieved” by $D = \delta Q$ where $\delta \rightarrow \infty$ and Q is any generator matrix with $\pi^\top Q = 0$ (π may be on the boundary).

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Ideal free dispersal – uncorrelated patches

- Suppose that Σ is a **diagonal matrix** (i.e. **zero correlations**) with diagonal entries $\sigma_{ii} = \sigma_i^2$.
- The **optimal dispersal distribution** is given by

$$\pi_i = \frac{1}{\sigma_i^2 \sum_j 1/\sigma_j^2} \left[\sum_j \frac{\mu_i - \mu_j}{\sigma_j^2} + 1 \right]$$

provided that $\sum_j (\mu_j - \mu_i)/\sigma_j^2 < 1$ for all i .

- **Ideal free dispersers visit all patches** provided that the environmental variation is sufficiently great relative to differences in the per-capita growth rates.

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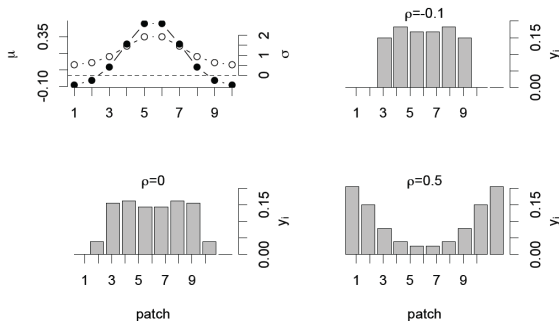
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Ideal free dispersal – a numerical example



Effects of **spatial correlations** on the ideal free distribution in a 10 patch environment. Mean per-capita growth rate μ_i and within patch variance σ_i^2 are plotted in the top left. The ideal free distribution π is plotted when there are **negative** ($\rho = -0.1$), **no** ($\rho = 0$) and **positive** ($\rho = 0.5$) **spatial correlations**.

A large dispersal rate approximation

- Suppose $D = \delta Q$, where Q is reversible with respect to π and consider what happens to $\chi = \chi(\delta)$ as $\delta \rightarrow \infty$.

- Recall:

$$d\mathbf{Y}_t = \delta Q^T \mathbf{Y}_t dt + \left(\text{diag}(\mathbf{Y}_t) - \mathbf{Y}_t \mathbf{Y}_t^T \right) (\mu - \Sigma \mathbf{Y}_t) dt \\ + \left(\text{diag}(\mathbf{Y}_t) - \mathbf{Y}_t \mathbf{Y}_t^T \right) \Gamma^T d\mathbf{B}_t.$$

- Define ν to be the solution of

$$Q^T \nu + (\text{diag}(\pi) - \pi \pi^T) (\mu - \Sigma \pi) = 0,$$

(note that Q is singular, but the existence and uniqueness of ν follows from spectral theory).

- Then, $\delta^{1/2}(\mathbf{Y}_{\delta^{-1}t} - \pi - \delta^{-1}\nu)$ converges to the solution of

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By standard facts about [Ornstein-Uhlenbeck](#) processes,

$$\begin{aligned} \chi(\delta) &\approx \left(\mu^\top \pi - \frac{1}{2} \pi^\top \Sigma \pi \right) \\ &\quad + \frac{1}{\delta} \left[(\mu - \Sigma \pi)^\top \nu \right. \\ &\quad \quad \left. - \frac{1}{2} \int_0^\infty \text{Tr} \left(\exp(Q^\top s) \left(\text{diag}(\pi) - \pi \pi^\top \right) \right. \right. \\ &\quad \quad \quad \left. \left. \Sigma \left(\text{diag}(\pi) - \pi \pi^\top \right) \exp(Qs) \Sigma \right) ds \right] \\ &\quad + O\left(\delta^{-\frac{5}{4}}\right) \end{aligned}$$

as $\delta \rightarrow \infty$.

A friendlier large dispersal rate approximation

- Suppose that Q is **symmetric** and $\Sigma Q = Q \Sigma$.
- Write $\lambda_1 \leq \dots \leq \lambda_{n-1} < \lambda_n = 0$ for the **eigenvalues** of Q with corresponding orthonormal **eigenvectors** ξ_1, \dots, ξ_n , where $\xi_n = \frac{1}{\sqrt{n}} \mathbf{1}$.
- Note that ξ_k is an **eigenvector** of Σ with **eigenvalue** θ_k , say.
- Then,

$$\chi(\delta) \approx \left(\bar{\mu} - \frac{1}{2n} \theta_n \right) - \frac{1}{\delta} \left[\sum_{k=1}^{n-1} \frac{1}{\lambda_k} \left(\frac{1}{n} (\xi_k^\top \mu)^2 - \frac{1}{4n^2} \theta_k^2 \right) \right] + O(\delta^{-5/4})$$

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Large dispersal rates – fully connected patches

- Suppose that $\Sigma = (1 - \rho)\sigma^2 I + \rho\sigma^2 \mathbf{1}\mathbf{1}^\top$ with $\rho \geq 0$ and $Q = n^{-1}\mathbf{1}\mathbf{1}^\top - I$.
- Then,

$$\chi(0+) < \chi(\infty-) \iff \frac{n}{n-1} \left(\max_i \mu_i - \bar{\mu} \right) < \frac{\sigma^2}{2}(1 - \rho).$$

- Also, $\chi(\delta)$ is **decreasing** for large $\delta \iff$

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Large dispersal rates – patches in a ring

- Identify the patches with the **integers modulo n** .
- Suppose $\mu = (1 + c, 1, \dots, 1)^\top$, where $c > 0$ (all patches are **equally good**, **except patch 0**, which is **better**), $Q_{ij} = q_{j-i}$ and $\Sigma = s_{j-i}$, where $q = (p_0 - 1, p_1, \dots, p_{n-1})$, with p is a probability vector for which $p_k = p_{-k}$, and $s = (1 + \eta_0, \eta_1, \dots, \eta_{n-1})$ for which $\eta_k = \eta_{-k}$.
- If $\max_i \eta_i$ is not too large, then there is a choice of c for which $\chi(0+) < \chi(\infty-)$ and $\chi(\delta)$ is **decreasing** for large δ , and **so intermediate dispersal is optimal**.

Large dispersal rates – patches in a ring

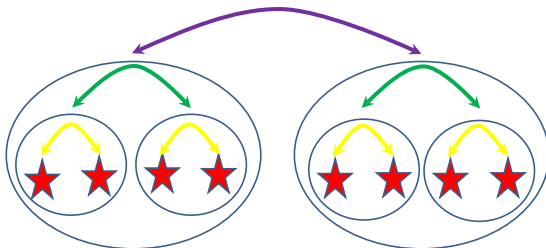
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- Suppose $\mu = (1 + c, 1, \dots, 1)^\top$, where $c > 0$ (all patches are **equally good**, **except patch 0**, which is **better**), $Q_{ij} = q_{j-i}$ and $\Sigma = s_{j-i}$, where $q = (p_0 - 1, p_1, \dots, p_{n-1})$, with p is a probability vector for which $p_k = p_{-k}$, and $s = (1 + \eta_0, \eta_1, \dots, \eta_{n-1})$ for which $\eta_k = \eta_{-k}$.
- If $\max_i \eta_i$ is not too large, then there is a choice of c for which $\chi(0+) < \chi(\infty-)$ and $\chi(\delta)$ is **decreasing** for large δ , and **so intermediate dispersal is optimal**.

Large dispersal rates – patches in a ring

- Identify the patches with the **integers modulo n** .
- Suppose $\mu = (1 + c, 1, \dots, 1)^\top$, where $c > 0$ (all patches are **equally good**, **except patch 0**, which is **better**), $Q_{ij} = q_{j-i}$ and $\Sigma = s_{j-i}$, where $q = (p_0 - 1, p_1, \dots, p_{n-1})$, with p is a probability vector for which $p_k = p_{-k}$, and $s = (1 + \eta_0, \eta_1, \dots, \eta_{n-1})$ for which $\eta_k = \eta_{-k}$.
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Large dispersal rates – hierarchically structured patches

It is possible to use representation theory to examine “topologies” such as patches arranged in a **hierarchy** (e.g. butterflies in bushes around meadows on islands).



Conclusion

Suitable probability models can shed light on how various dispersal strategies interact with environmental variability in time and space to influence population growth.

We have not accounted for the effect of competition for resources as population size increases.

Our model can be thought of as applying to situations where individuals are relatively scarce.

Also, $\chi > 0$ (resp. $\chi < 0$) in our model should be equivalent to the existence of a stationary distribution (resp. eventual extinction) after competition for resources is incorporated.