

# Schreiber Review

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## 1. Homogeneous populations

The mother of all single species ecological models: Births minus deaths minus emigration plus immigration,

$$N(t+1) - N(t) = G(N) = (B(N) - D(N) - E(N))N + I(N) \quad (1)$$

Notice immigration is only rate that is not per-capita. A CLOSED system has  $E = I = 0$ . PERSISTENCE requires  $G(N)$  have a positive derivative at zero. PERMANENCE is similar; the abundance each species present must always be greater than some (arbitrary) minimal amount. REGULATION requires the population not exceed some upper bound, which can only be accomplished by DENSITY DEPENDENCE: that is,  $B(N)$ ,  $D(N)$  are not constants but instead depend on the value  $N$  (Hixon et al. 2002, Ecology). When  $N \approx 0$ , a closed, persisting population grows geometrically (exponentially if continuous time) at a rate  $\lambda = B(0) - D(0)$ , i.e.  $N(T) = \lambda^T N(0)$ .

Density dependence implies that  $G(N)$  is nonlinear in  $N$ , and can be either POSITIVE (herd benefits, mate availability, resource protection), or NEGATIVE (competition, environmental modification, cannibalism). Negative density dependence must dominate at large  $N$  and keeps a population from getting too large. Positive density dependence that dominates at low  $N$  produces ALLEE effects, where a population below a certain size may be inviable (Courchamp et al., 1999, TREE). Tests for density dependence try to reject the null model that  $\log N_{t+1}$  is a linear function of  $\log N_t$  (we use logarithms because growth is multiplicative).

Single-species homogeneous populations can still do some weird stuff. These are all consequences of NONLINEAR DYNAMICS (read density dependence) ubiquitous to ecology (remember Hixon, regulation). MULTIPLE STABLE STATES, possibly exhibiting HYSTERESIS (meaning putting the parameters back the way they were before the shift to a different state doesn't make it switch back), and non-equilibrium steady states (LIMIT CYCLES) are possible examples. Most are discussed in Scheffer et al. 2001, Nature. These are examined using BIFURCATION DIAGRAMS, Fig 1. Simple models (one-dimensional discrete time) can give multiple stable states and CHAOS, (also viewed with bifurcation diagrams).

## 2. Temporal heterogeneity

Populations experiencing temporal heterogeneity can do even more weird stuff: like going extinct even though your expected population size goes to infinity, or betting on two losing strategies and winning. Temporal heterogeneity can be predictable (like seasons) or stochastic environmental variation; we focus on the latter. The general importance of the topic is outlined in Bjørnstad and Grenfell, Science 2001.

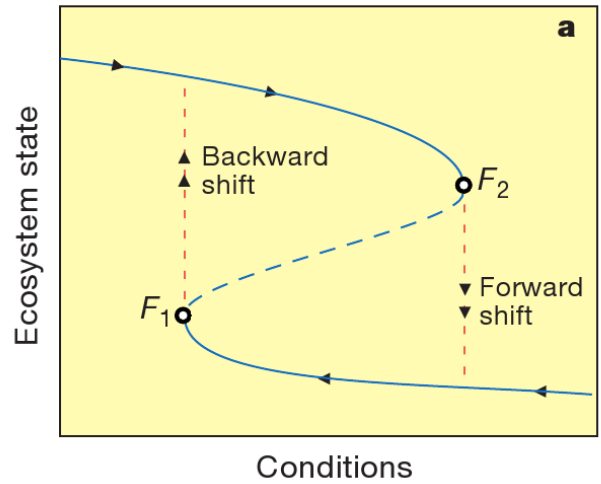


Fig. 1. bifurcation diagram exhibiting hysteresis, Scheffer 2001

### 2.1. Misleading means: Lewontin's favorite

If the fitness  $f_t$  (net per-capita offspring in the next generation) changes with time, the population size after some time  $T$  is:

$$N_T = f_T f_{T-1} f_{T-2} \dots f_0 N_0 \quad (2)$$

The expected population size  $E(N_T) = E(f)^T N_0$  if  $f$ 's are independent, identically distributed (i.i.d.) random numbers. We convert the products in Eq (2) to sums using logs,  $\ln N_T = \ln f_{T-1} + \dots + \ln f_0 + \ln N_0$ . In the long run (big  $T$ ) the "Strong Law of Large Numbers" lets us replace the sum of  $T$  i.i.d. variables with  $T$  times their average,  $E(\ln f)$ .

$$\ln(N_T) = TE(\ln f) + \ln N_0 \quad (3)$$

$$N_T = N_0 e^{TE(\ln f)} \quad (4)$$

In the long run, any given population grows at rate  $e^{E(\ln f)}$ , which is equal to the geometric mean,  $(\Pi_1^T f)^{1/T}$ . However the expected (read arithmetic mean population grows as  $E(f)$ ) The geometric mean is always less than the arithmetic.

As a good example, assume  $f$  on any year is equally likely to be  $f = 4$  or  $f = 1/8$ . The average,  $E(f) > 1$ , while the geometric mean is  $\sqrt{4 \cdot \frac{1}{8}} < 1$ , so the average population goes to infinity but any given population is guaranteed to go extinct!

This paradoxical behavior happens because any population which has not yet gone extinct is likely to be huge, even though most populations have gone extinct (and that one will too, if you wait

long enough); i.e. the distribution has very long tails. Some use the term INFLATION when the environmental variation increases the average population size; [Gonzales and Holt 2002, PNAS](#) discuss this, emphasizing that autocorrelated (instead of independent) noise can make the effect even bigger. (Article is over-hyped with applications from source-sinks to climate change.)

## 2.2. Bet Hedging example

Bet-hedging is really just another instance where you should just compute  $E(\ln f)$  to find out what is going to happen. Bet hedging means playing two (or more) losing games and ending up winning. If you can buffer the losses with a second, less variable option you can take advantage of the big wins from the more variable option. [Philippi & Seger 1989, TREE](#) provide an example with seed germination vs overwintering.

The example from the homework should illustrate this well. To compute the average of the log fitness we need to sum the logarithm of each of the possible fitness outcomes weighted by their frequency  $p$ . With payoff  $P_H$  for heads and  $P_T$  for tails in the variable environment, the fraction  $g$  of the population who played strategy 1, and  $s$  the survival chances in strategy 2, the expected log fitness is:

$$E(\ln f) = p \log(gP_H + (1-g)s) + (1-p) \log(gP_T + (1-g)s) \quad (5)$$

## 2.3. Population Viability Analysis

We've seen environmental (and demographic) stochasticity drive populations extinct even when their expected growth rate is positive. [Mangle & Tier 1994, Ecology](#), write "Four Facts Every Conservation Biologist Should Know:" (1) is our opening example, (2) says use their matrix method for PVA, (3) says catastrophes matter, (4) observes extinction times are exponentially distributed, so the majority of extinctions occur *before* the average extinction time.

## 3. Individual heterogeneity

Individual heterogeneity is about (age/stage) structured populations.

### 3.1. Leslie Matrices

Our favorite example is the loggerhead turtles, [Crouse et al. 1987, Ecology](#). This approach usually ignores density dependence, perhaps best for small populations (which makes nonlinearity weak).

Essential result is that whole matrix behavior can be mostly captured in a single number  $\lambda$ :

$$\mathbb{L}^t \mathbf{N}_0 \sim \lambda^t \mathbf{v} \quad (6)$$

LESLIE MATRIX:  $\mathbb{L}$  First row is the per-capita fecundity of each age class. The diagonals on the remaining rows are the fraction of that age class that survive into the next year but remain in that age class, while the term to the left are the fraction of the previous age class that will join that age class.

DOMINANT EIGENVALUE:  $\lambda$  (Perron eigenvalue), must be bigger than 1 for the population to persist.

STABLE AGE DISTRIBUTION:  $\mathbf{v}$ , (right eigenvector of  $\lambda$ ). Normalize the eigenvector (divide each element by the sum of all elements) to have these as fractions of the total population.

RELATIVE REPRODUCTIVE VALUE:  $\mathbf{w}$ , (left eigenvector).

SENSITIVITY: How big an effect an absolute change in a parameter has on the absolute value of  $\lambda$ , given by  $\frac{d\lambda}{da_{ij}} = w_i v_j$

ELASTICITY: How a relative change in a parameter effects the growth rate, given by:  $\frac{d\lambda}{da_{ij}} \frac{a_{ij}}{\lambda}$  (i.e., elasticity of 2 means 5% increase in  $a_{11}$  would give a  $2 \times 5\% = 10\%$  increase in  $\lambda$ .)

## 3.2. Extensions

LYAPUNOV EXPONENT: gives the divergence between the dynamic trajectories of two nearby initial conditions. Positive values indicate chaotic dynamics. [Constantino 1997, Science](#): nonlinear matrix models

[Silvia 1991, Ecology](#): Calculating Lyapunov exponents for burning grass

[Lloyd Smith et al. 2006 Nature](#): heterogeneous individuals have a big impact on disease dynamics: SUPER-SPREADERS.

## 4. Spatial heterogeneity

### 4.1. Metapopulation theory

The classic starting point is the LEVIN'S MODEL for METAPOPULATIONS. The world is divided into patches, a fraction  $p$  of which are occupied. Only some percentage  $h$  of the total patches are suitable for species (the rest have been turned into parking lots). Species colonize unoccupied patches at rate  $c$  and occupied patches go extinct at rate  $e$ .

$$\dot{p} = cp(h-p) - ep \quad (7)$$

A key conclusion from this LEVIN'S RULE (just solve for the equilibrium):  $h - \hat{p} = e/c$ , which says the fraction of unoccupied but suitable patches is equal to the extinction threshold,  $e/c$ . Persistence requires  $h > e/c$ , (positive  $\hat{p}$ ). Note  $e/c$  is  $h$  over the reproductive number of a patch (analogous to SIS disease model), is also analogous to the logistic equation).

Habitat fragmentation decreases  $h$ . The fraction of habitable but unoccupied patches,  $h - \hat{p}$  remains constant until  $h = e/c$ , below which the population goes extinct (hockey stick diagram).

RESCUE EFFECT: A modification of this model replaces  $e \rightarrow \frac{e}{1+mp}$ , which allows population to persist even if  $h < e/c$ .

Adding distance and area: the INCIDENT FUNCTION MODEL. Each patch  $i$  has an area  $A_i$  and a distance to patch  $j$  of  $d_{ij}$ . Smaller patches have higher extinction rates ( $e \sim 1/A^x$ ), and the fraction leaving a patch is proportional to its area (i.e. bigger patches have bigger populations, hence more dispersers). Hence colonization rate  $c_i$  of  $i$ th patch goes as  $\sum_j A_j e^{-d_{ij}}$  hence connectivity (distance) is more important than area.

[Hanski 1998, Nature](#), is a good review for this section.

### 4.2. Source-sink dynamics

Different definitions of sources and sinks and not being explicit about density dependence leads to a nuanced (confused) discussion in the literature. "Our" definition is that a population persists in a source, meaning it has a positive per capita growth rate near  $N = 0$ , while a sink does not.

[Pulliam 1988, Am Nat](#), requires sources positive per capita growth rate at some steady-state  $\hat{N}$ , which also means they have a net emigration. Trouble is, most articles forget density dependence – a patch can have different intrinsic growth rates at different densities  $N$ .

[Dias 1996, TREE](#) considers a population kept over its carrying capacity by net immigration a PSEUDO-SINK, and calls this process an INVERSION. Such a patch is a sink to Pulliam (net immigration) but a source to us (capable of persistence).

Both articles speculate that populations persisting in sinks are effectively extending the definition of niche.

#### 4.2.1. A general framework for metapopulations

Take as intrinsic per capita growth rate in patch  $i$ ,  $R_i(N_i) = B_i(N_i) - D_i(N_i)$ , and the emigration from patch  $i$  to other patches as  $E_i(N)$ , and  $\theta_{ij}$  is the contribution of the total emigration from the  $j$ th patch that goes to the  $i$ th patch:

$$R_i - E_i + \sum_j \theta_{ij} E_j \quad (8)$$

*Theorem: There is one unique  $\hat{N}$  that is stable.* Note that not all  $R_i$  can be greater than zero or less than zero for this to be stable. Then [Diffendorfer 1998](#), [Oikos](#) distinguishes between:

- (i) Pulliam style Source-sink dynamics, some  $R_i(\hat{N}) > 0$ , and some  $< 0$ .
- (ii) Or there is BALANCED DISPERSAL, where for all patches  $i$ ,  $I_i = E_i$ .

#### 4.3. Dispersal and Evolution

IDEAL FREE dynamics are a form of active dispersal where individuals go to patches which maximize their growth rate. This results in balanced dispersal at equilibrium, as described above. Dispersal is evolutionarily neutral, becomes unfavorable if there is any cost to dispersal.

PASSIVE DISPERSAL has all  $E_i$  equal. Evolutionary game theory shows the slower disperser always wins.

Temporal heterogeneity alone is selectively neutral to dispersal rates. *Both temporal and spatial heterogeneity are required for dispersal to be selectively advantageous, or to allow evolutionary coexistence of different dispersal rates.* Note: Coexistence with different dispersal rates is a common feature of ecological models that have only spatial heterogeneity. Consequently these models are not evolutionarily realistic, they only work because the model ignores the potential for evolution of dispersal rates in each population!

Experimental evidence that slower dispersers are favored using two *C. elegans*: [Friedenberg 2003](#), [Eco Let.](#) One strain is a mutant which goes in circles, and tends to do better unless there is both temporal and spatial heterogeneity.