Introduction to Population Dynamics

Marcus A.M. de Aguiar Lectures presented at the *Minischool on Dynamical Systems in Biology ICTP-SAIFR – May, 2014*

I – Linear models
II- Non-linear models
III – Spatial models
IV – Speciation
V – Sympatric speciation
VI – Spatial speciation

Population Dynamics

I. Linem Models

Consider A population of Annual plants, that produce an average of f seeds per plant in the summer and die in the winter. A fraction of the seeds also die during the winter and, of those that survive, only another fraction germinntes in spring and produce new plants. The number of plants in the year N+1 can be written As $P_{n+1} = \alpha \sigma f P_n \equiv r P_n (i)$ fraction Avenze number of fraction seeds per plant frat seeds that survives pe winth germine te

r = effective growth rate

This equation can be solved very easely by iteration: give the population at yen zens we obtain

$$P_{i} = \Gamma P_{0}$$

$$P_{2} = \Gamma P_{i} = \Gamma (\Gamma P_{0}) = \Gamma^{2} P_{0}$$

$$P_{3} = \Gamma P_{2} = \Gamma^{3} P_{0}$$
And
$$P_{n} = \Gamma^{n} P_{0} = P_{0} E^{n} M_{n} \Gamma$$
(a)

$$P_n = r^n P_0 = P_0 e^{-r}$$
(2)

If r>1 (lnr>0) we have an exponential growth of the population. If rel the population gets smaller and smaller, going extinct. Only for r=1 we obtain equilibrium, Pn=Po. In this first lecture we are foing to explore A set of equations that me very similar to eq. (1), In which the variable describing the populations occur only linemly (no Pn, cosPn, etc.). Although these equations are simple and can always be solved, tley involve some important aspects that we need to Know in some defail.

$$P_{n+1} = r P_n + m$$

I am going to modify eq. (1) shop by shop
so is to construct more interesting (med slightly
more complicitle) systems,
Migrants - Suppose that besides the plants growing
from last year seed's is number in of plants
gramme from extra seed brought by the wind,
The equilibrian becomes

$$P_{n+1} = r P_n + M$$
 (3)
This is a non-homogeneous complian and can be
solved by adding to the homogeneous solution
(for men) any particular solution of the fill
(for men) any particular solution of the fill
equiviend. The homogeneous compliants is solved
by eq. (n)
 $P_n = F_n f_n^n$

by eq. (c)
$$P_n = P_0 r^n$$

And A pmbiculin solution of eq. (3) is obtained by setting Pn = Pn+1 = P: $\overline{P} = \Gamma \overline{P} + M \implies \overline{P} = \frac{M}{1 - \Gamma}$

M

The complete solution is

$$P_n = P_0 \Gamma^n + \frac{m}{1-\Gamma}$$

As you can check by substituing. this the eq. 13).

$$P_n = i(P_0 - \frac{m}{1-r})e^{n lmr} + \frac{m}{1-r} \qquad (4)$$

Suppose now that pant of the seeds that did not germinich go through another winter and then have A second chance to do so. Our equation becomes

$$P_{n+1} = \alpha \sigma f P_n + \alpha' \sigma (1-\alpha) \sigma f P_{n-1}$$

when
$$(1-\alpha) = \text{fraction that did not germine le}}$$

 $\alpha' = \text{fraction of those two-years old}$
seeds that germinele

$$P_{n+1} - \beta P_n + \gamma P_{n-1} = 0$$
 (5)

where I the using $p = \alpha GF$ and $p = -\alpha G^2(1-\alpha)F$. This in A linear aquation of the second onder because it needs Pn and Pn-1 to find Pn+1. There are two ways of solving this aquation:

$$\frac{1 - \text{Direct solution}}{\text{vie try something similar to eq. (2):}}$$

$$P_n = C \lambda^n$$
where C and λ are unknowns. Substituting in (5):

$$C \lambda^{n+1} - P C \lambda^n + V C \lambda^{n-1} = 0$$
or

$$C \lambda^{n-1} (\lambda^2 - P \lambda + V) = 0$$
This is a good solution if

$$\lambda^2 - P \lambda + V = 0$$
(6)
otherwise C=0 or $\lambda = 0$ which is not what we are looking
for. Solving for λ we find two solutions

$$\lambda_{\pm} = -\frac{P}{2} \pm \frac{1}{2}\sqrt{P^2 + V}$$
(+)

And

$$P_n = C_+ \lambda_+^n + C_- \lambda_-^n$$
(8)

This is very similar to eq. (2) but now we need not only Po, but Also Pi to find to two constants Ct. And C. Exercise: Obtain expressions for C+ and C- in terms of the initial conditions Po mod PI.

Evample : the Fibomacci Rubbits You Are given
A couple of rubbits. It takes them one month to
method and, strating to second month they give
birth to one new couple every month. Assuming
every couple behaven the same way the number of rubbits
ever month, Fn, becomes:

$$F_0 = 0$$

 $F_1 = 1 \rightarrow first courle
 $F_2 = 1 \rightarrow 11$ II materia
 $F_2 = 2 \rightarrow first courle + Meand newly bern courle
 $F_4 = 3 \rightarrow 1st could + 2nd materia static beau
 $F_5 = 5$
 $F_6 = 8$
 \vdots
 $F_{VHI} = F_{II} + F_{II-1}$ (9)
Burgaring with eq. (5) we find (P=1, P=-1)
 $\lambda + = 1 \pm \sqrt{5}$$$$

$$\lambda_{\pm} = \frac{1 \pm \sqrt{5}}{2}$$

-

Using
$$F_0 = 0$$
 and $F_1 = 1$ we find
 $C_1 = \frac{1}{15}; C_{-} = -\frac{1}{15}$

And

$$F_n = \frac{1}{\sqrt{5}} \left(\frac{1+\sqrt{5}}{2} \right)^n - \frac{1}{\sqrt{5}} \left(\frac{1-\sqrt{5}}{2} \right)^n$$

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The Fibonacti numbers are very famous and the ratio between successive numbers is known to find to to "golden men", A proportion used in he Remaissance paintings and sculptures. It is defined as the way to divid a segment at 2 the three pmts X, I-X, I have So that ratio . fu sm x + x - 1 = 0 $\frac{1}{\chi} = \frac{\chi}{1-\chi} = 1$ $X = \frac{\sqrt{5}-1}{2}$

Exercise: Show find

$$F_n = \lambda_t = \frac{1}{\chi}$$

 $n \rightarrow \infty$ F_{n+1}

Eq. (5) can be re-written if we define
$$q_n = P_{n-1}$$
:
we obtain
$$\int P_{n+1} = \int P_n - \gamma q_n$$
$$\int q_{n+1} = P_n$$

which is a set of 2 equilions of the first order. This is avalogous to Newton's equation rewritten as Hamilhou's equations.

$$\int P_{n+1} = a_{11} P_{n+1} a_{12} q_{n}$$

$$\int q_{n+1} = a_{21} P_{n+1} a_{22} q_{n}$$

$$i + c_{n} b_{1} rewritten + s eq. (s) with$$

$$\beta = a_{11} + a_{22}$$

$$\beta = a_{11} + a_{22}$$

$$\gamma = a_{11} a_{22} - a_{22} a_{21}$$
(10)

with

$$X_{n} = \begin{pmatrix} P_{n} \\ q_{n} \end{pmatrix}, \quad A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}. \quad (12)$$

$$\beta = tr(A) = trace of A$$

 $\gamma = det(A) = determinant of A.$

If A is "well behaved" it has two spearle vectors Uf and U. , called ergenvector, such Emit

$$A \ \mathcal{J}_{\pm} = \lambda_{\pm} \mathcal{J}_{\pm}$$
(13)
$$A \ \mathcal{J}_{\pm} = \lambda_{\pm} \mathcal{J}_{\pm}$$

where the ergmunition λ_i satisfy $det (A - \lambda I) \equiv (a_{11} - \lambda)(a_{22} - \lambda) - a_{12}a_{21} \equiv 0$. This is exactly eq. (6) with the definitions (10). Once λ_{+} and λ_{-} are alculated, eqs. (13). on be solved for U_{+} and U_{-} . The solution of equilion (11) is given by

$$X_{N} = \alpha_{+} \lambda_{+}^{N} \mathcal{J}_{+} + \alpha_{-} \lambda_{-}^{N} \mathcal{J}_{-} \qquad (14)$$

PROOF

$$A X_n = \alpha_i \lambda_i^n A J_i + \alpha_i \lambda_i^n A J_i$$

 $= \alpha_i \lambda_i^{n+1} J_i + \alpha_i \lambda_i^{n+1} J_i$

Xn+1

It is important to understand this structure, II The plane P-q is usually called the "phase space". A point in this plane represents the populations at a given moment.

Vectors represent directions in the plane. The

vector $\mathcal{U}_{1} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$



the interve $P - Attis in The vector <math display="block">M_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$

is in the q-direction. Finally consider

$$\mathcal{M}_{3} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

mod the set of points a. Us for OKaKO. It spans the line passing through the origin and the point (P, q) = (1,1).

Similarly the digenvectors
$$\nabla_{\pm}$$
 and t .
represent special directions in this plane. If
the initial consistion are chosen so that $Q_{\pm}=0$
in eq. (14) then
 $X_{n+1} = Q_{\pm}\lambda_{\pm}^{n+1} \nabla_{\pm}$
and the solution moves along the line defined by Φ_{\pm} .
If $Q_{\pm}=0$, the points γ_{\pm} move along U_{\pm} . The
type of motion defines on whether λ_{\pm} and λ_{\pm}
are possitive, negative, smaller or limps them 1,
and on complex.
The behaviour of the solutions (8) on (14) on
be studied if we focus on the contribution of each
 $M_{\pm} = Q_{\pm} \lambda_{\pm}^{n}$
 Q_{\pm}

where λ is one of the two solutions $\lambda + on \lambda - a$ The following cases my Appen According to eq. (7)



In this case $\lambda_{+} = \lambda_{-}^{*}$ and we need to take both term into account. Consider eq. (8); because Puts read we need to choose $C_{+} = C_{-}^{*}$.

Setting

$$\lambda_{\pm} = \frac{B}{2} \pm \frac{i}{2}\sqrt{48-p^{2}} \equiv r \frac{i}{2}q$$

$$\Gamma = \sqrt{8}$$

$$t_{9}q = \frac{\sqrt{48-p^{2}}}{B}$$

$$C_{\pm} = \frac{A-iB}{2}$$
, $C_{\pm} = \frac{A+iB}{2}$

we get

0

$$P_{n} = \frac{(A - iB)}{2} r^{n} e^{n} + \frac{(A + iB)}{2} r^{n} e^{n} e^{n}$$

 $P_n = A r^n w (n e) + B r^n sin (n e).$



Example: production of red blood alls

$$R_{n} = normbar of blood all of dry n
M_{n} = normbar of alls produced by Marrow on day n
F = fraction of alls removed by sphen
 $0 = \text{production constant} (\# of alls produced
per all removed)
R_{n+1} = (1-f)R_n + M_n
M_{n+1} = 0fR_n
(a) R_{n+1} = (1-f)R_n + YfR_{n-1}$$$

$$(b) \left(\begin{array}{c} R_{n+1} \\ M_{n+1} \end{array} \right) = \left(\begin{array}{c} (l-f) & l \\ m_n \end{array} \right) \left(\begin{array}{c} R_n \\ m_n \end{array} \right)$$

$$(M_{n-1}) | \forall f = O/(M_{n})$$

$$U_{si-g} | (a) with R_{n} = C \lambda^{n} leads h$$

$$\lambda^{2} - (i-f)\lambda - \delta f = 0$$

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$$\lambda_{\pm} = \frac{1-f}{2} \pm \frac{1}{2}\sqrt{\Delta}$$

$$\Delta = (1-f)^{2} \pm 4\pi f > (1-f)^{2}$$

$$\Rightarrow \lambda_{\pm} > 0$$

$$\lambda_{\pm} < 0$$
and $|\lambda_{\pm}| > |\lambda_{\pm}|$

$$R_{n} = C_{1}\lambda_{\pm}^{n} \pm C_{2}\lambda_{\pm}^{n}$$
For large n to behavior is dominated by λ_{\pm} .
To maintain a coustable number of and blood cells
we need to have $\lambda_{\pm} = 1 \pm \frac{1}{2}\pi \sum_{k=1}^{n} \sqrt{D} = 1 \pm f$

$$\Omega = (1-f)^{2} \pm 4\pi p = (i+f)^{2} \Rightarrow \sqrt{D} = 1 \pm f$$

$$\Omega = (1-f)^{2} \pm 4p = (i+f)^{2} \Rightarrow \sqrt{D} = 1$$

$$i.e., for each all distroyed we need parting$$

on all produced.

· · · ·

$$\frac{\text{Exercise}}{\text{eqs}(1) \text{ and } (2)}, \text{ the plants three if the humber of seeds produced per plant satisfies for the satisfies is $f > \frac{1}{\sqrt{2}}$$$

SO that IN . If seeds from the previous year also "contribute to the population, as an eqs. (5) med (8), show that this condition become

And less needs are needed. Hent: impose >+>1.

Other examplis

1) Insects. Each female has f offsprint; A fraction m dres before maturity; A fraction I of the offspring are females

$$P_{n+1} = \Gamma(1-m) f P_n$$

2) Predators
$$P_n$$
 and $preys q_n$
 $P_{n+1} = dP_n + aq_n$
 $q_{n+1} = rq_n + bP_n$

Solve to problem Assuming

$$d = 1/2$$
, $r = 3/2$, $b = 3/2$, $a = 5/2$
While your solution in terms of 90 , $P0$.

Solution:
$$\lambda_{+} = 5/2$$
 $\lambda_{-} = -1/2$
 $U_{+} = \begin{pmatrix} 2/3 \\ 1 \end{pmatrix}$ $U_{-} = \begin{pmatrix} -4/3 \\ 1 \end{pmatrix}$

$$\mathcal{M}_{n} = \begin{pmatrix} P_{n} \\ q_{n} \end{pmatrix}$$

$$\mathcal{M}_{n} = \begin{pmatrix} P_{0} + q_{0}/3 \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n} \mathcal{J}_{\pm} + \begin{pmatrix} 2q_{0} - r_{0} \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n} \mathcal{J}_{\pm}$$

$$\mathcal{M}_{n} = \begin{pmatrix} P_{0} + q_{0}/3 \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n} - \frac{1}{3} \begin{pmatrix} 2q_{0} - r_{0} \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n}$$

$$\mathcal{M}_{n} = \begin{pmatrix} P_{0} + q_{0} \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n} - \frac{1}{3} \begin{pmatrix} 2q_{0} - r_{0} \end{pmatrix} \begin{pmatrix} \tau_{\pm} \end{pmatrix}^{n}$$

$$\mathcal{M}_{n} = \begin{pmatrix} P_{0} + q_{0} \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n} + \begin{pmatrix} 2q_{0} - r_{0} \end{pmatrix} \begin{pmatrix} \tau_{\pm} \end{pmatrix}^{n}$$

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$$\mathcal{M}_{n} = \begin{pmatrix} P_{0} + q_{0} \end{pmatrix} \begin{pmatrix} \Xi \\ \Xi \end{pmatrix}^{n} + \begin{pmatrix} 2q_{0} - r_{0} \end{pmatrix} \begin{pmatrix} \tau_{\pm} \end{pmatrix}^{n}$$

$$\lim_{n \to \infty} \frac{q_n}{p_n} = \frac{3}{2}$$

Population DyNAMICS

I. NON-Liner Models

Linear models of population dynamics are not very replicities in at least one ancial respect: the population either grow forever or go extinct. Stability is attained only is very special conditions which me untikely to be satisfied. If we go batcle to eq. (I.1) Prize I Ph we can try to fix the problem by limiting the growth rate r is the population gets too ling. One was to do that is setting

$$P_{n+l} = \frac{K P_n}{b + P_n}$$
(1)

Becase A complete solution of A NON-linem
equivition is not generally possible we adopt A
different strategy. Let
$$X_{n+1} = f(X_n)$$
 (2)

represent a generic pon-linen equation for the population X. Here is what we do:

The equation to solve is

$$X = f(x)$$
2) Study to dynamic in the vicinity of
this solutions. If $\overline{X}_{1} = f(\overline{x})$ we
avoid $X_{12} = \overline{X}_{1} + 8X_{12}$ (3)
where $8X_{12}$ is a small deviation from \overline{X}
at granting n . What is the population
at $n+1$? If $8X_{12}$ is small we
expect $X_{n+1} = \overline{X} + 8X_{n+1}$ (4)
If $[8Y_{n+1}] > [8Y_{n}]$ to dynamic is
pushing the population array from the equilibrium
and \overline{X} is an unstable equilibrium. If
 $[8Y_{n+1}] < [8Y_{n}]$ to dynamic is moving

the population back towards
$$\overline{X}$$
, and the 4
point is STABLE.
Replacing (3) and (0) in (2):
 $\overline{X} + 8 \times_{n-1} = f(\overline{X} + 8 \vee n)$
 $\overline{X} + 8 \times_{n-1} = f(\overline{X}) \perp 8 \vee n \frac{2f}{2x}(\overline{X})$
 $= \overline{X} + 8 \vee n \frac{2f}{2x}(\overline{X})$
 $= \overline{X} + 8 \vee n \frac{2f}{2x}(\overline{X})$
where used $f(\overline{X}) = \overline{X}$ and $\frac{2f}{2x}(\overline{X})$ is the
densation of f evaluated at \overline{X} . Thus have
 $8 \vee n_{11} = 8 \vee n \frac{2f}{2v}(\overline{X})$ (5)
and we have a simple activity for h subsidily of
 \overline{X} is stab if $\left[\frac{2f}{2x}(\overline{X})\right] < 1$ (6)

X is vushable if Df (x) > 1

eq. (1). The equilibria me solutions of

$$P = KP$$

 $b + P$

 $\overline{P}(J+\overline{P}) = \overline{F} = \overline{P}$

Then are two solutions:
$$\overline{P}_0 = 0$$

 $\overline{P} = K - b$.

Stability Analysis needs
$$\frac{\partial f}{\partial P}(\overline{P})$$
 where $f = \frac{KP}{b+P}$
 $\frac{\partial f}{\partial P} = \frac{K}{(b+P)^2} = \frac{KB}{(b+P)^2}$

For the equilibrium point
$$\overline{P}_0 = 0$$
 $\Im_F(\overline{P}_0) = \frac{1}{2}b_0$.
For $\overline{P} = K - b$ we find $\Im_F(\overline{P}) = \frac{1}{2}b_K$. Therefore,
if $K < b$ extinction is a stable solution and
if $K > b$ the population will converge to $\overline{P} = K - b$.
Graphically we have



P

The denominator introduced in eq. (1) has the effect of Limiting the total population that the region can support. Another way of including this property is by setting

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$$P_{n+1} = \Gamma P_n (1 - P_n/k)$$
.

Once ASMIN the growth rate r(1-Ph/K) depends on the population and decreases as Pn -> K. Defining Xn = Pn/K = population in units of K

we obtain
$$X_{n+1} = r X_n (1 - X_n)$$
. (7)

This equation is known as the logistic equation and has been studied by many people. It has incredibly complicited behavior and was popularized by Robert Muy. I am going to briefly discuss som of its properties here but the render can find a lot of instead about it on the web.

- equilibrium solutions Setting f(x) = rx(1-x) = x we find $\overline{X}_0 = 0$ $\overline{X}_r = 1 - Vr \Rightarrow positive only for r>1$

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- stability

$$\frac{df}{dx} = r - 2r \times \Rightarrow \begin{cases} for \ \overline{X}_0 = 0 \\ for \ \overline{X}_r = 1 - f \\ dx \end{cases}$$

$$for \ \overline{X}_r = 1 - f \\ dx \end{cases}$$

Therefore, for orral the solution $\overline{X}_0 = 0$ is stable and Xr is unstable. From the biological point of view Xr should not be considered in this interval, since it is negative. For I<r<3 Xo is Unstable, since Et) and Xr is stable. However, if $\Gamma > 3$, 3Ay $\Gamma = 3+E$, $2-\Gamma = -1-E$ And Idf)>1 for Xr as well and the population will no reach an equilibrium! However, as long is f(x) is Always bounded between r<4,

And I, and the population oscillates in the interval OXXXI on OXPXK:



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Exactse: TAKE r=3.3, $X_0=0.5$ and calculate the "orabit" X_1, X_2, X_3, \cdots

Solution		$X_0 = 0.5$		
		$X_{1} = 0.825$ $X_{2} = 0.476$	Kh A A A A A A A A A A A A A A A A A A A	
		$X_3 = 0.823$ $X_4 = 0.480$	5 8	
		X= = 0.824		
		X6= 0.479		
		X7=0.021		

The population derrily oscillates between two values, 0.48 and 0.82. We can find these points explicitly with the following trick:

$$X_2 = f(X_1)$$
 and $X_1 = f(X_2)$

then, Applying the dynamics three returns to some - fruit - fruit point :

$$X_{i} = f(X_{2}) = f[f(X_{i})].$$

Explicitly we obtain

$$f(x) = r \times (1-x)$$

$$f(f(x)) = r f(x) (1 - f(x)) = r [r \times (1-x)] [1 - r \times (1-x)]$$
And we need to solve

$$r^{2} \times (1-x) [1 - r \times (1-x)] = X . \qquad (8)$$
This is a polynomial of degree 4 and to solutions

Mre

1)
$$\overline{X}_{0} = 0$$

2) $\overline{X}_{r} = 1 - V_{r}$
3) $\overline{X}_{\pm} = \frac{r + 1 \pm \sqrt{(r - 3)(r + 1)}}{2r}$
(9)

Solution X_{\pm} are the ones we are looking II for. It can be checked that $f(X_{\pm}) = X_{\pm}$

And that they a real only for r>3. Are these equilibria of the "two-sleps equifion" stable? To figure this out we need to calculate

$$\lambda = \frac{d}{dt} \left[f(f(n)) \right] = \frac{d}{dt} \left(f(n) \right) \frac{d}{dt} (x)$$

$$x_{t}$$

$$= \frac{df}{dx}(x_{+})\frac{df}{dx}(x_{-}) \qquad (10)$$

$$(11 \quad x = x_{+}, \quad f(x) = x_{-} \quad \text{and} \quad v(u - verse). \quad We \quad get$$

$$\lambda = (r - 2r X_{+})(r - 2r X_{-}) = 1 - (r - 3)(r + 1) . (11)$$

For
$$r=3.3$$
 we find $\lambda = -0.29$, which shows that
this "period two" oscillation is shall. For $r=3.5$ we
obtain $\lambda = -1.25$ which indicates instability. To find
out exactly the actual r we re
 $1 - (r-3)(r+1) = -1$

And find r= 1+16 = 34495

The bifurcation diagram, similar to

that on PASI 6, becomes



After r= 1+16 the population oscillates between four values and then bifurcates again to an 8-points solutions and so on. News soon a cascad of bitures take place and the dynamics Very soon a cascad of bitures take place and the dynamics become very complicated. For more see Robert Devancy, An Introduction to Cheotic Dynamical Systems.

Exercises: Solve eq (8) and demonstrate (10) and (11).

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$$X_{n+1} = f(X_n, y_n) \qquad (12)$$

$$y_{n+1} = g(X_n, y_n) \qquad .$$

Here the functions f and g describe the interactions between the two species. The equation are usually very hand (or impossible) to solve and we follow the idea hand (or impossible) to solve and we follow the idea of finding the equilibria and study their stability. Of finding the equilibria and study their stability. $\overline{X} = f(\overline{X}, \overline{Y})$ (B) $\overline{Y} = g(\overline{X}, \overline{Y})$

To study its stability we consider small
deviations and while
$$X_n = \overline{X} + \overline{X}_n$$

 $\overline{y}_n = \overline{y} + \overline{y}_n$

And Also write

$$X_{n+1} = \overline{X} + \overline{Y}_{n+1}$$

 $y_{n+1} = \overline{y} + \overline{y}_{n+1}$.

We obtain

$$\overline{x} + \overline{x'}_{n+1} = f(x_{n+1}\overline{x'}_{n}) \overline{y}_{n+1}\overline{y'}_{n}$$

 $\overline{y} + \overline{y'}_{n+1} = g(x_{n+1}\overline{x'}_{n}) \overline{y}_{n+1}\overline{y'}_{n}$
Expanding the functions $f \text{ and } \overline{y}_{n+1}\overline{y'}_{n}$
And \overline{y}_{n+1} (13) we find
 $\overline{x'}_{n+1} = \alpha_{n} \overline{x'}_{n} + \alpha_{n} \overline{y'}_{n}$
 $\overline{y'}_{n+1} = \alpha_{n} \overline{x'}_{n} + \alpha_{n} \overline{y'}_{n}$
 $\overline{y'}_{n+1} = \alpha_{21} \overline{x'}_{n} + \alpha_{n} \overline{y'}_{n}$
(14)
 $\overline{y'}_{n+1} = \overline{\beta}_{1}(\overline{x}, \overline{y})$
 $\alpha_{12} = \overline{\beta}_{2}(\overline{x}, \overline{y})$
 $\alpha_{12} = \overline{\beta}_{2}(\overline{x}, \overline{y})$
 $\alpha_{21} = \overline{\beta}_{2}(\overline{x}, \overline{y})$
 $\overline{\gamma}_{2}(\overline{x}, \overline{y})$

azz = 33 (I, 1)

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with
$$W_{n+1} = A W_{n}$$

with $W_{n+1} = \left(\begin{array}{cc} \chi_{n} & Q_{12} \\ Q_{21} & Q_{22} \end{array} \right)$, $A = \left(\begin{array}{cc} Q_{11} & Q_{12} \\ Q_{22} & Q_{22} \end{array} \right)$.

This is exactly the type of Linean System we discussed in page 9-15. Stability is determined by

the eigenvalues

$$\lambda_{\pm} = \frac{\beta}{2} \pm \frac{1}{2} \sqrt{\beta^{2} - 4\gamma}$$

$$\beta = \alpha_{11} + \alpha_{22}$$

$$\gamma = \alpha_{11} \alpha_{22} - \alpha_{12} \alpha_{21}$$

(I) If. 40 > B'
$$\lambda_{\pm}$$
 are complex and can
be written as $\lambda_{\pm} = re$ with $r = \sqrt{p}$.
Therefore $|\lambda_{\pm}| < |i_{\pm}| < |i_{\pm}|$ $p < |.$ (see Mg. I-14)
(II) IF
$$4p < p^{2}$$
 be are read.
(A) IF $p>0$ be and be set
"dominant eigenvilue". Stability requires
 $\lambda_{+} < 1$:
 $\frac{p}{2} + \frac{1}{2} \sqrt{p^{2} - 4p} < 1$
(A1) $p < 2$, otherwise $\lambda_{+} > 1$
(A1) $p < 2$, otherwise $\lambda_{+} > 1$
(A1) $p < 2$, otherwise $\lambda_{+} > 1$
(A2) $p + \sqrt{p^{2} - 4p} < 2 \Rightarrow p - 2 > \sqrt{p^{2} - 4p}$
on $p^{2} - 4p < p^{-4}p + 4 \Rightarrow 8>p^{-1}$
(A3) $4p < p^{2} < 4 \Rightarrow p < 1$
(A3) $4p < p^{2} < 4 \Rightarrow p < 1$
Putting all together we set that the condition
(for $p>0$) is
 $p - 1 on $p
(B) If $p < 0 > \lambda_{-} < \lambda_{+} < 0$ and we
need $\lambda_{-} > -1$. We obtain
 $1p < 1 < p > 1$ condition
for statisticty.$$

EXAmples

where $H_n(1+aI_n/r)^k$ is the fraction of hosts Hny /F

where
$$H_{n}(1 + \alpha I_{n}/\kappa)^{k}$$
 is the finction of hosts
surviving the parasition. Re-writing
 $I_{n+1} = H_{n} - H_{n+1}/F$
Equilibrium solutions are
 $(\overline{H}, \overline{P}) = (0, 0) \rightarrow \text{stable if } F < 1$
or
 $\left(\overline{H} = \left(\frac{F}{F-1}\right) \stackrel{k}{=} (F^{V_{k}} - 1)^{k}$
 $\overline{P} = \stackrel{k}{=} (F^{V_{k}} - 1)$

For this point we find

$$F = 1 + \frac{k}{F-1} + \frac{F^{1/k} - 1}{F^{1/k}}$$

$$\gamma = k \left(\frac{F^{1/k} - 1}{F^{1/k}} \right) \left(\frac{F}{F-1} \right).$$

(3) Plant - Herbivores

$$\int_{n+1} = f \sqrt{n} e$$

$$\int_{n+1} = r h_n \left(8 - \frac{h_n}{\sqrt{n}} \right)$$

$$f_1 r_1 s_1 a > 0,$$
(a) Show that $\overline{r} = \frac{rh}{r^{s-1}}$; $\overline{h} = \frac{h_n f}{a}$ is

An equilibrium solution,

(b) Define: $V_n = \sqrt{n}/\sqrt{r}$, $H_n = h_n/\sqrt{n}$ and show

that H_0 equiphers become

 $V_{n+1} = V_n e$

 $H_{n+1} = bH_n \left[1 + \frac{1}{b} - \frac{H_n}{\sqrt{n}} \right]$

Where k = lmf, b = rS - 1. (c) $Draw a dragram in the <math>b \times K'$ plane showing to regions where the equilibrium point H = V = 1 are stable.

19 Competion for the same resources between two species; $\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha N_2}{K_1} \right)$ $\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \beta N_1}{K_2}\right)$ d, p are degrees of interference of one species on the other. (9) In traguild Predation = N, and No comple for the same resources and N, pre-dates Nr.

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha N_2}{E_1} \right) + \gamma N_1 N_2$$

$$\frac{dN_{L}}{dt} = r_{2}N_{2}\left(1 - \frac{N_{2}-\beta N_{1}}{K_{2}}\right) - SN_{1}N_{2}$$

.

(5) Epidemics - the SIR model 20

$$S = considerable individuals$$

$$I - in factod individuals$$

$$R = reconserved$$

$$\frac{dS}{dE} = -(BIS)$$

$$\frac{dI}{dE} = (BIS - VI) = 3) S + Ir R = N = und.$$

$$\frac{dR}{dE} = VI$$

$$\frac{dR}{dE} = VI$$

$$\frac{dR}{dE} = VI$$

$$\frac{dR}{dE} = ir th incubation pariod$$

$$\frac{dS}{dE} = ir th rely = diath m(s)$$

$$\frac{dS}{dE} = \mu N - \mu S - (SIS/N)$$

$$\frac{dE}{dE} = P IS - (N + \alpha)E$$

$$\frac{dR}{dE} = \alpha E - (V + \alpha)I$$

$$N = S + E + 3 + R - 6ul.$$

(7) The quasi-species equation

Consider n''species " specified by n genoms 3, 32, ... In . The frequency of genome i is

Ri And

$$\frac{dx_i}{dt} = \sum_{j=1}^{\infty} X_j f_j q_{ji} - \Phi X_i$$

where

$$\phi = A Verage fitness of contractions of cont$$

- SHOW THAT THIS COVATION IS UNSISTENT with $2 \times i = 1$.

Population Dynamics

III. Spatial Models

So far we have considered the time evolution of systems at discrete time steps, from time n to time n+1. Also, we have only been concerned with the total number of individuals of each species motived. If the populations are longe and if individual may die or be born at any time, it makes more sense to us! a continuous time approach. In the case of the logistic equilibrium, for example, we could write dN = TN(I-NIK) (1)

where F now is the avery number of offspring per individual per unit time (for example 2 offspring per individual per year).

$$N(t) = \frac{K}{1 + (\frac{K}{N_0} - 1)e^{-rt}}$$

Ehrt converges to K for my interl condition:
ONE VARIABLE - The general equation describing a
single population has the form:

$$\frac{dN}{dt} = f(N)$$
(2)

- equilibrium requires
$$f(\overline{N}) = 0$$

- stability is obtained by withing $N = \overline{N} + n$ and
expanding to finish on den
 $\frac{dn}{dt} = \frac{\partial f(\overline{N})}{\partial N} = E N$.

Ch

$$h(t) = n_0 e$$

Therefore
$$\overline{N}$$
 is shall if $\overline{E} < O$ and
unshall if $\overline{E} > O$. (compare with lar in eq. $\underline{L}(2)$)

Two VARIABLES - If I and Q represent two
interacting populations, then

$$\frac{dP}{dt} = f(I,0)$$

$$\frac{d0}{dt} = g(I,0)$$

$$\frac{d0}{dt} = g(I,0)$$

$$\frac{d0}{dt} = g(I,0)$$

$$\frac{d0}{dt} = g(I,0)$$

$$\frac{d0}{dt} = g(I,0) = 0$$

$$f(I,0) = g(I,0) = 0$$

$$= setting I = I + P, \quad 0 = \overline{0} + g \text{ no obtain}$$

$$\frac{dW}{dt} = AW ; \quad W = \begin{pmatrix} P \\ q \end{pmatrix}$$

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{2}{2}f & \frac{2}{2}g \\ \frac{2}{2}f & \frac{2}{2}g \end{pmatrix}_{P,\overline{0}}$$
(4)

solution 15 The with= GI Jie + GJ vie hit $A \sigma_1 = \lambda_1 \sigma_1$ (2)A JZ= X2 JZ $W(0) = W_0 = C_1 J_1 + C_2 J_2$. The equilibrium $\widehat{P}, \widetilde{Q}$ is still if the rul part of both A, and A. are negative. For more vaniables the method is the same, only EL JACOBIAN Matrix A gets lage A classic example is the Lotka-Volterry model for A prey P and A predator Q: $\frac{dr}{dt} = \frac{xP}{4} - \frac{PD}{4}$ exponential decrense due to () pre dation growth $\frac{d\theta}{dt} = -\gamma Q + S 2 Q$ death in the population growth Absince of food If the me prey.

The two equilibrius and corresponding Theolon 5
unknown are:
(o) Extinction
$$\overline{P} = \overline{Q} = 0$$
 $A = \begin{pmatrix} \alpha & 0 \\ 0 & -\gamma \end{pmatrix}$
eigenstein $\overline{A}_1 = \alpha > 0$ $A = \begin{pmatrix} \alpha & 0 \\ 0 & -\gamma \end{pmatrix}$
eigenstein $\overline{A}_1 = \alpha > 0$ $A = \begin{pmatrix} \alpha & 0 \\ 0 & -\gamma \end{pmatrix}$
(b) Co-existence $\overline{P} = \gamma/8$ $\overline{D} = \alpha/\beta$
 $A = \begin{pmatrix} 0 & -\gamma \sqrt{8} \\ \alpha & \beta \end{pmatrix} \rightarrow \overline{A}_1 = \varepsilon \sqrt{\alpha}\gamma$
 $A = \begin{pmatrix} 0 & -\gamma \sqrt{8} \\ \alpha & \beta \end{pmatrix} \rightarrow \overline{A}_2 = -\varepsilon \sqrt{\alpha}\gamma$
The equilibrium is "manginally shelt", with
remaining solutions oscillation moved it.
Equiptions (6) on actually be integrated and
we find that
 $Q^{\alpha} = \overline{PQ} = \frac{c}{2} \frac{e}{2}\gamma$
where C is A constant. The behavior is illustented

below:



SPACE AND DIFFUSION

In many servicions it is not enough to know the tobel populations and information about its spatial distribution many be important. The usual approach to include space is to assume that interactions between individuals occur locally and that individual move around by diffusing, or by other mechanisms, such as following scents or other cues, For the logistic equition we would wark

$$\frac{\partial N(y,t)}{\partial t} = r N(y,t) \left[1 - N(y,t)/k \right] + \frac{\partial 2^{2} N(y,t)}{\partial x^{2}}$$

for un space-dimension n and when D is the diffusion wefficient. This agention has the infinishing property that the homogeneous (spre independent) solution we wroke down in proje 2 is still a solution, since Siviox'=0 The question as really whether the presence of diffusion changes the stability character of the solution. When a stable solution of a space independent problem becomes bushable because of diffusion, non triving space dependent solutions may arise, generating what is known as TURING PATTERNS.

DIFFUSION

Diffusion is the re-arrangement of pankicles (or individuals) due to their random motion. In a gas, for example, pankicles move around randomly and for example, pankicles move around randomly and panticles on a dense region will naturally move towards regions with lower densities.

Consider à one-dimensional pipe that we

divide into little segments of size DX

K K+I

We define the flow At K As the number of particle that cross the boundary K/K+1 per unit time:

J

$$J(K) = DN(K, KH)$$

And the density of particles at segment K AS

$$g'(\kappa) = \frac{N(\kappa)}{DX}$$

If S(K) VANIES in time is because there are publicles Mossing the K-1/K and K/K+1 boundaries:

$$\frac{\Delta P(k)}{\Delta t} = \frac{-\Delta W(k, k+1) + \Delta W(k-1, k)}{\Delta X \Delta t}$$

$$= \frac{J(k) - J(k-1)}{\Delta x} = -\frac{\Delta J}{\Delta x}$$

If the number of particles coming in and out is the same the density does not change. In the limit where DX-DO, Dt-DO this becomes

$$\frac{\partial f}{\partial t} + \frac{\partial x}{\partial J} = 0 \quad . \quad (f)$$

We now use "Fick's Low" which sty that the flow of panticles is proportional to the spatial variation of the density:

$$J(x) = -D \frac{\partial x}{\partial x}$$
(8)

So that if
$$S$$
 is constant then is no flow. If
the "diffusion coefficient" D is constant wo find
 $\frac{\partial f}{\partial E} = \frac{D \partial^2 f}{\partial x^2}$. (3)

Notice the minun sign in eq. (8), stying that the flow is from the high density to the low density regions. In 3-D this generation to

$$\frac{\partial f}{\partial t} = D\left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} + \frac{\partial^2 f}{\partial 3^2}\right) = D\nabla^2 f.$$

Exacuse : show that

$$g(x_{it}) = \frac{1}{\sqrt{4\pi}Dt} e^{-\frac{x^{2}}{4}Dt}$$

is a solution of eq. (9) and draw $\mathcal{P}(x,t)$ for $t \approx 0$ and t > 0.

TURING PATTERNS

We have going to see how Turing patterns with Using the model of Minura & Murray (J. Theor. Bist. 75 (1978) 249). It is similar to the Lotka-Voltern model of prey P and preditors Q:

$$\frac{\partial P}{\partial t} = \left(\frac{a+bP-P^2}{c}\right)P - QP + D_P \frac{\partial^2 P}{\partial x^2}$$
(10)

$$\frac{\partial 0}{\partial t} = -(1+e0)Q + IQ + D_0 \frac{\partial^2 Q}{\partial x^2}$$

where P(x,t) and Q(x,t) are densities of pregs and productors at position x and time t; D_P and D_Q are the diffusion coefficients. And $0 \le x \le L$.





The constant coefficients will be fixed at
$$a=35$$
, $b=16$, $c=9$, $e=2/5$.

Homogeneous Equilibrium

Setting
$$\frac{\partial P}{\partial t} = \frac{\partial Q}{\partial t} = 0$$
 leads to equilibrium solutions.
Setting function $\frac{\partial P}{\partial x} = \frac{\partial Q}{\partial x} = 0$ liads to spatially
homogeneous solutions $\overline{P}, \overline{Q}$:
 $\overline{D} \left[\left[\frac{a+b\overline{P}+\overline{P}}{2} \right] - \overline{Q} \right] = 0$

$$\overline{O}\left[-1-e\overline{O}+\overline{P}\right] = 0$$

There are 3 solutions:

$$(\overline{P}, \overline{Q}) = (0, 0) \rightarrow \text{ extinction}$$

$$(\overline{P}, \overline{Q}) = (\frac{b}{2} + \frac{1}{2}\sqrt{5^{2}4}e^{2}, 0) = (8+\sqrt{99}, 0) \rightarrow \text{ only progs}$$

$$(\overline{P}, \overline{Q}) = (5, 10) \rightarrow \text{ co-existen } (1, 5) \text{ lothom of}$$

$$(\overline{P}, \overline{Q}) = (2, 10) \rightarrow \text{ co-existen } (2, 5) \text{ lothom of}$$

$$(\overline{P}, \overline{Q}) = (2, 10) \rightarrow \text{ co-existen } (2, 5) \text{ lothom of}$$

$$(\overline{P}, \overline{Q}) = (2, 10) \rightarrow \text{ co-existen } (2, 5) \text{ lothom of}$$

In order to study the stability of
these solutions we need to specify the boundary
conditions at
$$\chi=0$$
 and $\chi=1$. We assume that
there is no flow of individuals through the
boundaries (see eq. (B)) i.e.,
 $\frac{\partial f}{\partial \chi}(0) = \frac{\partial f}{\partial \chi}(L) = \frac{\partial Q}{\partial \chi}(L) = 0$

These conditions are obviously satisfied by the homogeneous solutions, since they do not depend on χ . Therefore we look for perturbations $Q = \overline{Q} + q$ (11) $P = \overline{P} + q$

with
$$\frac{\partial q}{\partial x} = \frac{\partial P}{\partial x} = 0$$
 At $x=0, L$.

$$P(x,t) = \sum_{n=1}^{\infty} a_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) = \sum_{n=1}^{\infty} P_n(x,t)$$

$$P(x,t) = \sum_{n=1}^{\infty} b_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) = \sum_{n=1}^{\infty} q_n(x,t)$$

$$P(x,t) = \sum_{n=1}^{\infty} b_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) = \sum_{n=1}^{\infty} q_n(x,t)$$

$$P(x,t) = \sum_{n=1}^{\infty} b_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) = \sum_{n=1}^{\infty} q_n(x,t)$$

$$P(x,t) = \sum_{n=1}^{\infty} b_n e^{\lambda t} \cos\left(\frac{n\pi x}{L}\right) = \sum_{n=1}^{\infty} q_n(x,t)$$

This corresponds to the decomposition of A general noisy function into A sum of simple periodic functions, each of them satisfying the boundary conditions. Moreover we can think of these modes as acting one at a time and the effect of the total perturbation is going to be the sum of the effects of each mode separately. (Prove this!).

EACH mode (Phr. 9n) has a typical "size", or Wavelength (13)

$$L_n = \frac{2L}{n} \tag{13}$$

For h=5, for example, we find



What we want to find is for what values of M, or for what Lenght Ln, the exponent & becomes positive and the perturbation grows, destroying the homogeneous solutions and creating regions of high density separated by regions of low density, i.e., patterns.

We set Do= & and DP= (for simplicity. Later we will set d=1 so that (is is the diffusion of preys measured in term of the diffusion nate of the predators.

$$\frac{\partial P_n}{\partial t} = \alpha_{11} P_n + \alpha_{12} q_n + \beta \frac{\partial P_n}{\partial x^2} \qquad (14)$$

$$\frac{\partial q_n}{\partial t} = \alpha_{21} P_n + \alpha_{22} q_n + \chi \frac{\partial^2 q_n}{\partial x^2}$$

where

$$\begin{aligned} a_{11} &= \frac{\alpha + b\overline{P} - \overline{D}^{2}}{c} + \overline{I} \left(\frac{b - 2\overline{P}}{c} \right) \\ a_{12} &= -\overline{P} \end{aligned} \tag{15}$$

$$\begin{aligned} a_{21} &= \overline{Q} \\ a_{22} &= \overline{Q} \\ a_{22} &= \left[\overline{P} - (1 + e\overline{Q}) \right] - e\overline{Q} \\ \overline{Q} \\ \frac{\partial^{2} P_{n}}{\partial x^{2}} &= - \alpha_{n} e^{\lambda} \left(\frac{n\pi}{L} \right)^{2} \cos \left(\frac{n\pi + \lambda}{L_{n}} \right) \\ &= - \alpha_{n} e^{\lambda} \left(\frac{n\pi}{L} \right)^{2} \cos \left(\frac{2\pi \times}{L_{n}} \right) = - \nabla_{n} P_{n} \end{aligned}$$

$$\frac{\partial^2 q_n}{\partial x_n} = -\overline{G_n} q_n$$

$$\mathcal{T}_n = \left(\frac{NTT}{L}\right)^2 = \left(\frac{2TT}{Ln}\right)^2$$

.

$$\frac{\partial P_n}{\partial t} = \left[Q_{11} - \beta \sigma_n \right] P_n + Q_{12} P_n$$

$$\frac{\partial Q_n}{\partial t} = Q_{21} P_n + \left[Q_{22} - \alpha \sigma_n \right] Q_n$$

If there were no diffusion, $\alpha = \beta = 0$ we would be back at the non-linem non-spalial case.

In this case we find that: - EXTINCTION is unstable - only pregs is unstable - co-existence is stable

For this last equilibrium we find

$$a_{11} = \frac{30}{9}$$

 $a_{12} = \frac{-5}{9}$
 $a_{21} = \frac{10}{9}$
 $a_{22} = -4$

The JACobian matrix has digenvalues

$$\lambda = -\frac{1}{3} \pm i\sqrt{329}$$
Showing that the population "spirals" back
be the homogeneous equilabrium.
Setting $\alpha = 1$ we obtain , for the
fill JACobian matrix,
 $\lambda_{\pm} = \frac{1}{2} \pm \frac{1}{2}\sqrt{5^2 + 2}$
 $b = a_{11} + a_{22} - Gn(1+\beta) = -\frac{2}{3} - Gn(1+\beta)$
 $c = (a_{11} - \beta Gn)(a_{22} - Gn) - a_{12}a_{21} = \frac{110}{3} - Gn(\frac{20}{3} - 4\beta)$
 $+ (\beta Gn^2)$

The idea is to calculate $\lambda \pm$ for each value of n and check if $|\lambda_{\pm}|$ in $|\lambda_{\pm}|$ can be Imperture of destabilizing the homogeneous sublish. Results from the paper are shown next:









For small
$$\beta$$
, like $\beta = 0.0125$ in
figure 2, the lowest mode to general instability
is $N=3$. The simulation in fig. 3
Shows the mithal partonbation to the homo-
geneous solution $\overline{P}=5$, $\overline{Q}=10$ as two
Kinks at $x=L/2$ and the resulting stationary
pattern, with 3 regions of high prop durity and
3 with low prop durity.
It is subgrising that diffusion, which thats
to homogenize the distribution has excelling the
opposite effect here, of creating non-homogeneithm.
This phynomenon was discovered by Alm Turing
and is known as Turing Pattern, and the
mechanism TURING ENSTABILITIES.

Start from

 $\dot{\hat{q}} = f(\hat{r}, \hat{q}) + D_{\hat{r}} \frac{3\tilde{r}}{3\chi^2}$ $\dot{\hat{q}} = g(\hat{r}, \hat{q}) + D_{\hat{q}} \frac{3\tilde{q}}{3\chi^2}$

PROVE	9F	STATE	MENT
 IN PA	Ge l'	4	

and set $P = P_0 + \frac{2}{n} P_n$ $q = q_0 + \frac{2}{n} q_n$

Linux Rising we obtain $Z_{n} \hat{P}_{n} = f_{p} Z_{n} \hat{P}_{n} + f_{q} Z_{n} \hat{q}_{n} + D_{p} Z_{n} \frac{\partial \hat{P}_{n}}{\partial x}$ $Z_{n} \hat{q}_{n} = \partial_{p} Z_{n} \hat{P}_{n} + \partial_{q} Z_{n} \hat{q}_{n} + D_{p} Z_{n} \frac{\partial \hat{q}_{n}}{\partial x}$ $Z_{n} \hat{q}_{n} = \partial_{p} Z_{n} \hat{P}_{n} - f_{q} \hat{q}_{n} - D_{p} \frac{\partial \hat{P}_{n}}{\partial x} = 0$ $Z_{n} \left[\hat{P}_{n} - f_{p} \hat{P}_{n} - f_{q} \hat{q}_{n} - D_{p} \frac{\partial \hat{P}_{n}}{\partial x} \right] = 0$ $Z_{n} \left[\hat{q}_{n} - \hat{q}_{p} \hat{P}_{n} - \hat{q}_{q} \hat{q}_{n} - D_{p} \frac{\partial \hat{q}_{n}}{\partial x} \right] = 0$

Thur fore, if $\dot{r}_n = f_e P_n + f_q q_n + D_e \frac{\partial^2 P_n}{\partial x_1}$ $\dot{q}_n = g_e P_n + g_q q_n + D_e \frac{\partial^2 q_n}{\partial x_1}$

for each n, the full equation is satisfied.

SPECIATION

I. ALLOPATRY X SYMPATRY

The dynamical models we have discussed so for occur at the so-called "ecological" time scale, A so fficiently short time in leaved when evolutioning charges can be ignored. Now I want to consider systems where the internetic characteristics of a species (like its growth rale) can charge because it got better adapted to its invironment.

During the DovA replication mutations on occur As a result of ocasional arrows, or due to exposure to radiation, lithium and other chemicals. If this mulations occur on a sex cell they can be transmitted to offspring. Although most mulations are bad, some of them there out to be useful for the individial at that time, making them "fitter" them others without the mulation, i.e., helping them have more offspring and pross to mulation on. The mechanism that makes "good" mutations be incomporated in the population and "bad" mutations be disconded is called NATURAL SELECTION, A term coined by Charles Dominin.

Small Adaptitions can lead to big changes over the years, As allow tracked by the evolution of wholes:



In sevent occasions there is more than just big changes: there are bifurcations, or speciation, and new species are formed:



4

SPECIES - For our purposes species will be defined using the concept of reproductive isolation. A species is a group of individuals that an interamony chanselies but not with individuals of other such groups. In An abstract "genetic space" species are islands separated from each other by gaps that are long enough to prevent inter-islands reproduction. We don't require that every mult in a species and with every fimile. There might be some incompatibilities inside a species, as long as each individual on mile with a few others in the species.

ALLO PATRIC SPECIATION

A series of empirical observations pointed to the fact that "sister species" - species that are close relations - were often separated by each other by geoprophial barries. Example:

(A) each side of the Isthmus of Panam has I specin of shrimp. Each specin has its closed relative on the other side

(B) Drossphille's specin in Hawaii Islands (c) Danwin's finches in the Galapagos islands

i i

There is also a famous experiment by Dian Dodd where dissophilles was exposed to stanch or melhose. After many generations each group adapted to its environment and, when the population were re-mixed together they would only male with others of the same group.

Is geographic isolation the only why to rach reproductive isolation? Many scientistic thinks so, Although less stringent barriers have been considered. The term <u>pars patric speciation</u> was coined to describe situations where partial barrier decrease the which between subpopulations without completely blocking gene flow. There are basically two classes of propatric models

- CLINAL SPECIATION

continuous habitate with an environmental gradient leading to local Adaptations.

The local Adaptations might let d to t discrete elevators instead of a continuum of phenotypes.

The other extreme of Allopatric speciation there is sympatric speciation, where mating is not restructed at All by glographic barriers but might respond to ecological competition.

SYMPATRIC SPECIATION

Here I will us the model by Dieckman & Debeli (Nature 400 (1992) 354) to discuss how competition on lead to the break up of population into two reproductively Isolated growups in the same spatial location. Suppose a population of binds lives on area where seeds of sevent sizes are available. The amount of seeds of size 5, 9(5); in distailable in such a way that there are lots of "average" size seeds and less big on small seeds. We can think of a more distailed in such of

The binds, on the other hand, are 8
chreacterized by a quantitative trait
$$x$$
 which
Messawi back size. We assume that binds
with bait x follow a logistic growth expension
with sile appearing $K(x)$ whose shore
dollows the distribution of resources
 $\frac{1}{\sqrt{2}} \frac{1}{\sqrt{2}} \frac$
modeled by

C(n, v) = e

so that the more similar the series, the more induse the competition.

Assume that initially a small population with
Erail
$$\kappa$$
 colonizes the new. The population growth
can be modeled with a logistic equation
 $\frac{d}{dt} N(n,t) = r N(n,t) \left[1 - \frac{N(n,t)}{\kappa(n)} \right]$
After a time of the order of $1/r$ the
population inches its appreciation and
 $N(n,t) \longrightarrow K(n)$

(see eq. II. (2) .

9

The question we want to ANSWER is : what 10 Imppens if a notant with phenotype

Appears? Will It "invade" and take over to may?

The Answer seen pretty obvious: if K(v) > K(n) the motants should do well, since they can est more seeds that the residents. We will see that there is more to it than just that.

$$\frac{d V(y,t)}{d t} = \Gamma V(y,t) \left[-\frac{C(y,y)K(x)}{K(y)} \right]$$

Since of sels an "efective population" C(n,v) K(n) competing for the same resources.

$$-8\pi/2\sigma_{c}^{2}$$

 $C(n, S) = e' = \pi - \frac{8\pi}{2\sigma_{c}^{2}},$

to first order in
$$\mathcal{E}_{\mathcal{R}}$$

$$\frac{d N(y_i,t)}{d t} = r N(y_i,t) \left[1 - \frac{K(y_i)}{K(y_i)} \right] = R N(y_i,t)$$

$$R = r\left(1 - \frac{k(n)}{k(n)}\right) > 0$$

DISRUPTIVE SELECTION

Since the population shifts towards $\mathcal{H}=0$ independent of its founder phenotypes, let us consider what happens to a mutant that appends when the residents have $\mathcal{H}=0$.

In this case the ratio
$$8\pi^2/25E^2$$

$$\frac{K(n)}{K(y)} = \frac{K(y)}{K(y)} = e = 1 + \frac{8\pi^2}{25E^2}$$

ALSO deffers from 1 by O(Sic) and we cannot discand competition. The full R is

$$R = \left[\left[1 - \frac{k(n)C(n, y)}{k(y)} \right] \right] x = 0$$

$$y = \delta n$$

$$= r \left[1 - e^{\frac{8\pi^2}{26\kappa^2} - 8\pi^2/26\kappa^2} \right]$$
$$= r \left[1 - e^{\frac{8\pi^2}{26\kappa^2} \left(6\kappa^2 - 6\kappa^2 \right)} \right]$$

Therefore, if
$$\sigma_{k} > \sigma_{c}$$
.

R>O and the population of mutant grow.



Sympatric Speciation

Summary

- Speciation mechanisms: allopatry x sympatry
- The model of Dieckmann & Doebeli
- Sex



Seleção Natural



Charles Darwin 1809-1882



SOCIÉTÉ EL CÉOGRAPHIE MAULLA FOX, PIRIS LONDON.

Alfred R. Wallace 1823-1913

Evolution by natural selection



Evolution versus Speciation



Speciation





Allopatry: the basic mechanism of speciation



Geographic isolation leads to Reproductive isolation.

Classic example: Darwin finches on the Galápagos islands



T=ground, A=tree, V=vegetarian, C=singer

Example: cichlid fishes in lake Victoria (Tanzania, Africa)



There are approximately 400 species of cichlids with a common ancestral that lived about 14 thousand years ago.



No evident geographic separation.

Is speciation possible without geographic isolation?

On the origin of species by sympatric speciation

Ulf Dieckmann & Michael Doebeli

Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria Zoology Institute, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

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Competition and Disruptive Selection

z = trait associated with resources \rightarrow beak size

resources are seeds, whose quantity depends on seed size

birds with similar beak size compete for seeds



Resources are finite and its distribution dictates how many birds of each beak size are possible:

$$K(z) = K_0 \exp\left[-\frac{z^2}{2\sigma_k^2}\right]$$



z=0 is the beak size corresponding to the most aboundant seed

Competition: individuals with similar phenotypes compete. The strength of competition is modeled by a Gaussian function:

$$C(z,w) = \exp\left[-\frac{\left(z-w\right)^2}{2\sigma_c^2}\right]$$



birds with beak sizes in the interval $z\text{-}\sigma_{c}\text{---}z\text{+}\sigma_{c}$ compete significantly with z

Single population with beak size z:

$$\frac{dN(z,t)}{dt} = rN(z,t) \left(1 - \frac{N(z,t)}{K(z)}\right)$$

$$N(z,t) = \frac{N(z,0)K(z)}{N(z,0) + \left[K(z) - P(z,0)\right]e^{-rt}} \rightarrow K(z)$$

What happens if a mutant with beak size $w = z + \delta z$ appears?

$$\frac{dN(w,t)}{dt} = rN(w,t) \left(1 - \frac{C(z,w)K(z)}{K(w)} \right) \equiv RN(w,t)$$

$$C(z,w) = \exp\left[-\frac{\left(z-w\right)^2}{2\sigma_c^2}\right] = \exp\left[-\frac{\delta z^2}{2\sigma_c^2}\right] = 1 - \frac{\delta z^2}{2\sigma_c^2}$$

$$R \approx r \left(1 - \frac{K(z)}{K(w)} \right)$$

As expected, if K(w) > K(z) the effective growth rate is R > 0 and the mutant grows and invades the population.

If K(w) < K(z) then R < 0 and the population of mutants decreases.

The result is that a small mutation rate makes the population evolve towards the maximum carrying capacity z=0, where more food is available.

What happens when the population gets there?

z = 0

 $w = 0 + \delta z = \delta z$

$$R = r \left(1 - C(0, \delta z) \frac{K(0)}{K(\delta z)} \right) = r \left[1 - e^{-\delta z^2/2\sigma_c^2} e^{\delta z^2/2\sigma_k^2} \right]$$

Therefore, if

$$\sigma_k > \sigma_c$$

R > 0 and the **mutants** $w = 0 + \delta z$ **AND** $w = 0 - \delta z$ both grow and invade the z = 0 phenotype!

If competition is too strong, it might be advantageous to have a more extreme phenotype, where there are less resources, but also less competition:



Asexual Individual Based Model

- each individual has phenotype -1 < x +1
- reproduction occurs at rate r
- death rate is

$$\frac{1}{K(x)}\sum_{y}N(y,t)C(x,y)$$

• offspring inherit the parent phenotype, but mutations occur with probability μ . In that case x is chosen from a normal distribution with average x and variance σ_u =0.05.

r=1, K₀=500, σ_k =1, μ =0.001



Figure 1 Convergence to disruptive selection **a**, Evolutionary branching in the individual-based asexual model: at the branching point $x_0 = 0$, the population splits into two morphs. Three insets show fitness functions (continuous curves) generated by the ecological interactions at different points in time (indicated by horizontal dotted lines). Selection changes from directional to disruptive when evolution reaches x_0 . The resource distribution K(x) has its maximum at x_0 and is shown for comparison (dashed curve). **b**, As in **a**, but with multilocus genetics for the ecological character and random mating. Shading represents phenotype distributions (5 diploid and diallelic loci result in 11 possible phenotypes). Despite disruptive selection at the branching point (see insets), branching does not occur.

Sexual Model

Ecological character (beak size) is attributed according to 5 diploid biallelic loic



Reproduction:

Result from simulations: population does not branch. Intermediate phenotypes keep showing up.

Sexual Model with assortative mating

Besides the ecological character, two other genetic traits are attributed to the individual, each with 5 diploid biallelic loci:

 $\begin{array}{l} + + - + + + \\ - + - + + + \\ - - + + + \\ - - - + + + \\ - - - + + + \end{array} \quad m = mating \ preference \ trait: \qquad \begin{array}{c} -1 = mate \ with \ opposite \\ 0 = no \ preference \\ +1 = mate \ with \ similar \end{array}$

If mating preference refers to the ecological trait, the dynamics leads to the fixation of m close to +1, i.e., to the evolution of positive assortativity for individuals with similar ecological character. This avoids the mixture of extreme phenotypes and results in disruptive selection as in the asexual model.



If preference is with respect to the neutral character (color of feathers), the dynamics still leads to the evolution of positive assortativity, mating with individuals with similar neutral character.

The population splits in two groups according to the neutral character. However, each group also has a different ecological character: blue feathers go with small beak and red feathers with large beak (or vice versa). The time it takes for splitting, however, is almost 10 times larger.



Speciation in spatially extended populations

Allopatry: the basic mechanism of speciation:



Geographic isolation leads to Reproductive isolation.

Classic example: Darwin finches on the Galápagos islands



T=ground, A=tree, V=vegetarian, C=singer

Another example: Cichlid fishes in lake Victoria (Tanzania, Africa)





There are approximately 400 species of cichlids with a common ancestral that lived only 14 thousand years ago.

Super fast speciation. No geographic barriers. No evidence of strong competition.
Geography and Genetics work together in Evolution

Dramatic examples of their intertwined roles are provides by *RING SPECIES*, where the population is restricted by partial geographic barriers



Greenish Warblers Birds in the Tibetan Plateau

Figure 1 Geographic range of the greenish warbler species complex, along with research sites and representative song spectrograms. Different colours illustrate the ranges of six taxa commonly considered to be subspecies of *Phylloscopus trochiloides*⁴: purple, *nitidus*; blue, *viridanus*; green, *ludlowi*; yellow, *trochiloides*; orange, *obscuratus*, red, *plumbeitarsus*. Colours grade together in regions where Ticehurst⁴ described gradual change between subspecies. Research sites are indicated by their two-letter designation.

Also shown are representative song spectrograms (horizontal axis is time, vertical is frequency, darkness is amplitude) from eight locations⁷. Letters and brackets below the spectrograms indicate distinct song units. Song structure (for example, length of each unit, repetition of units, frequency range) differs between *viridanus* and *plumbeitarsus*, but there is a gradient in song around the southern side of the ring⁷.

Salamander, Ensatina (California)



Hering Gull (polar circle)



Euphrobia Tithymaloides (plant)



Figure 2. Documented populations of *E. tithymaloides* in the Caribbean are represented in full circles, colour-coded by subspecies. The 42 populations included in this study are marked with an asterisk and have been assigned names representative of their localities.



FIG. 1. The 16 sample locations for *Aulostomus* species. By conventional distributions, *A. maculatus* inhabits the West Atlantic, *A. strigosus* inhabits the East Atlantic, and *A. chinensis* inhabits the Indian and Pacific Oceans. *Aulostomus chinensis* was collected from: (1) Isla del Coco (Pacific Costa Rica, n = 9); (2) Easter Island (n = 5); (3) Clipperton Island (n = 5); (4) Hawaii (n = 15); (5) Guam (n = 18); (6) Ningaloo Reef (West Australia, n = 7); (7) Reunion Island (n = 7); and (8) Punta del Orro (Mozambique, n = 2). *Aulostomus strigosus* was collected from: (9) São Tome (Gulf of Guinea, West Africa, n = 16); (10) Cape Verde (n = 16); (11) St. Helena (n = 19); (12) Ascension Island (n = 19); and, based on a revision of species distributions (13) St. Paul's Rocks (Brazil, n = 14) and (14) Espirito Santo (Brazil, n = 22). *Aulostomus maculatus* was collected from: (15) Florida Keys (U.S.A., n = 15); and (16) Belize Barrier Reef (n = 7).

Summary

- Speciation without barriers
- Partial barriers and Ring species
- Future directions

1. Speciation without barriers

a) finite population with initially identical individuals randomly distributed in space



L

periodic boundary conditions

b) haploid and hemafroditic individuals with genome represented by a sequence of B loci with two alleles

One Haploid Genome

1	1	0	1	0	0	1	1	1	0	1	0	0	0	1	1	0	1	0	1	1	1	0	0	1
1	2	3	4	5	•	•		•	•	b	it r	nun	nbe	er	•		•	•						В

- (c) sexual reproduction occurs only if:
 - individuals are not too different genetically (G)
 - individuals are not too distant from each other (S)

Genetic distance:



- (c) sexual reproduction with recombination and mutation occurs if:
 - individuals are not too different genetically (G)
 - individuals are not too distant from each other (S)



Recombination and Mutation (diploid phase)



 μ = mutation rate

(d) The total number of individuals in the population is kept constant.

(e) Initial condition: population of genetically identical individuals

0 0 0 0 0 0 0 0 0 0 0

- (f) at each generation every individual tries to reproduce, but there is a probability Q that it will not make it. In this case a neighbor is chosen to reproduce in its place. The total number of individuals in the population is kept constant.
- (g) Offspring can be placed exactly at position of the dying individual with probability (1-D) or somewhere nearby with probability D.

Time Evolution Measured in Number of Generations



Number of Species as a function of time





Genetic distance from individuals of the same species as measured from the center of population





Trees in Panama Tropical Forest (BCI)





2. Partial barriers and Ring Species

Ayana B. Martins IB-USP Yaneer Bar-Yam – NECSI – Boston Marcus A.M. de Aguiar

Greenish Warblers Birds in the Tibetan Plateau

Irwin et al Science (2005)

Genetic distances and geographic distances are strongly correlated.

We conclude that there is no break in gene flow through the ring of populations.

Genetic continuum seems to be unstable and ring might soon break down into separate species.





Figure 1 Geographic range of the greenish warbler species complex, along with research sites and representative song spectrograms. Different colours illustrate the ranges of six taxa commonly considered to be subspecies of *Phylloscopus trochiloides*⁴: purple, *nitidus*, blue, *viridanus*; green, *ludlowi*; yellow, *trochiloides*, orange, *obscuratus*, red, *plumbeitarsus*. Colours grade together in regions where Ticehurst⁴ described gradual change between subspecies. Research sites are indicated by their two-letter designation.

Also shown are representative song spectrograms (horizontal axis is time, vertical is frequency, darkness is amplitude) from eight locations⁷. Letters and brackets below the spectrograms indicate distinct song units. Song structure (for example, length of each unit, repetition of units, frequency range) differs between *viridarus* and *plumbeitarsus*, but there is a gradient in song around the southern side of the ring⁷.















Principal Component Analysis



First principal component





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