

Ecology and Evolution

BI2113

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Fall 2020

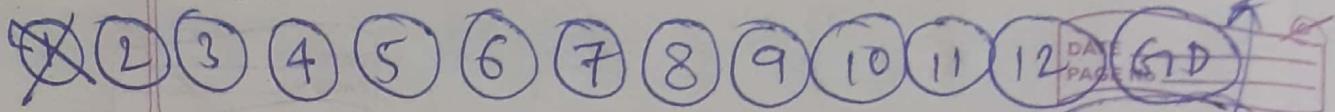
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1 Introduction

ECOLOGY & EVOLUTION

Serengeti



(C1) Wildebeest → Tanzania (Serengeti)
grassland

↓
animal migration (~1500 km)

↓
a lot will die due to starvation,
disease, hunting, predators while
on the way

rain
water

most efficient muscles among
mammals (62.5%)

special muscle

Special adaptation

i) Reproduction

ii) Babies

one male can get many

- Mating season → begin in May
- Don't form permanent bond due to their migratory behaviour
- Temporary territory
- Birthing period → Jan - May

birth in middle of herd

baby → can learn to run quickly

- NB:
- They're super abundant > all herbivores in system combined
 - move for food
 - Prefer short grass

depends on rain

- GPS → location & coordinate
- they need to leave a place because Serengeti doesn't have proper irrigation system & dries out quickly
- if they are tracking food, then they should go towards its direction ideally

- Acc. to GPS collar, they follow rainfall
- river crossing in way
↓ (Marosmer)
cool.

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- pred. 1 - variation in space & availability of food

Acc. to GPS collars → both are true

Is migration the reason behind the large no.? Yes!

- Not all WB migrates
- Migration gives WB more food
- 80% death from
- Resident WB → 80% death → predators
- Migrant WB → 25% death → ?? {who?}
- Predators can't follow migrating herd

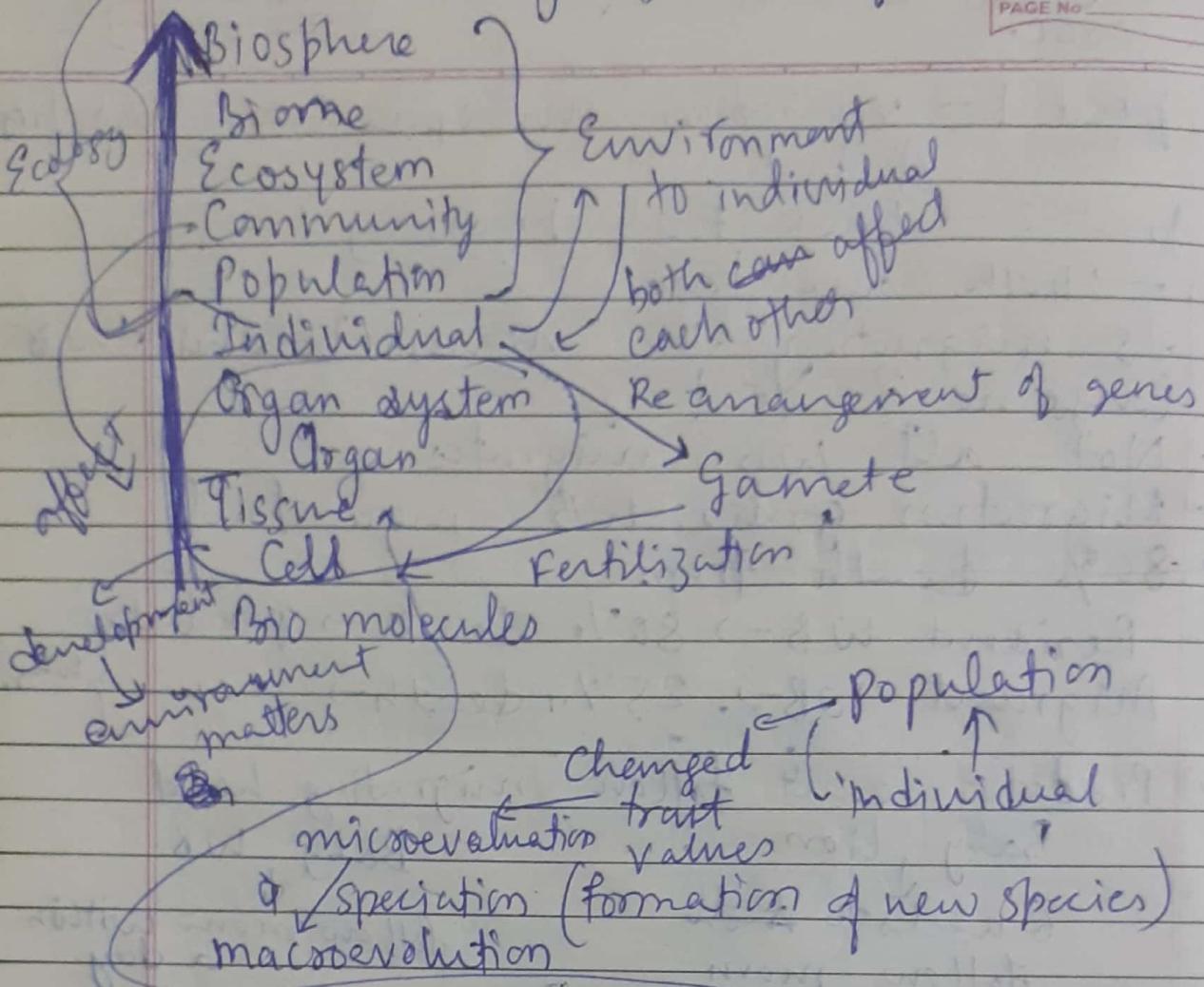
Baby lion
↓
6 weeks to ~~1 month~~
follow mom

Baby WB
↓
follow mom within a day

- have more density
- migrating animals → large no.'s
 - WB helps maintain ecosystem
 - every year, their carcasses produces P → 13 tons, N → 25 tons, C → 107 tons
 - WB migration → increases tree cover & benefits ecosystem
 - as WB population ↑ what causes it
 - as WB population ↑ ⇒ area of forest burn ↓ fire
 - Elephant popu. ↑: more trees needs dry grass

- Why bio is so structureless or heavy?
- Structural organization of life

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- environment also changes
- even a small change here can cause big difference later
- We can't ever get exact same replicate condition, hence biological systems → are instantaneous (mostly about individual and higher levels, not for biomolecules)

→ Diversity & interconnectedness:

- 1) within a level
 - 2) across levels
- Stochasticity: Cheesy, cheezy world
 - Historicity: What had happened affects what will happen
 - Replaying the tape of evolution: Allowing evolution to happen again from same

Starting conditions

- Emergence - reductionism often fails
 - When we are unable to explain something happening at higher level with by considering what's happening at lower level
- reductionism becomes difficult, it's difficult to come up with mathematical formulation.
- When possible, relation with reality is typically difficult statistical & conditional which leads to other issues
- no two individual is same, hence difficult to p account.

→ Then what to do? Two ways -

- 1) just figuring out what is there (description)
- 2) trying to build simplified models with all kinds of caveats (lim. predictive power)

- don't go for maths, instead go for verbal models
- instead of quasi quantitative, go for qualitative model
- go for simple & focused model

→ What will we do?

↳ oversimplified

1. Oversimplified mathematical modeling
2. focus on concepts
3. historical narrative → own teaching?
4. Examining the pedagogy

→ fundamental trade off: breadth vs depth
we choose breadth

Mandatory reading → for exams

2 Structured Population

Chapter 2, Part 1 :-

→ Ecology :- coined by Ernst Haeckel (1866) :-
 oikos ("house") + logia ("study off")

↳ interactions between organisms and environment.

Biotic ↔ Abiotic
 (Living) (non living)

Why do we study populations -

IMP Facts:- India to overtake China in 7 years

In last decade, Syria lost 20% of its population.

Human Demography :- Subset of population ecology

Group of similar individuals
 in a defined space at given time.

Why to study non-human populations :-

- Conservation of endangered species
- Management of economically important species
- " " " harmful species
- Fundamental unit of evolution.

What population ecologists study :-

- Distribution → How individuals are distributed over space
- Demography → Age structure, survivability etc.
- Dynamics → Change of the numbers over space and time.

Population Dynamics :-

what patterns are observed, why are they achieved

1st Example :-

Herb called Phlox drummondii

To study the dynamics :-

First we define a specific space, and then count the number of individuals in that space.

Next, define a unit of time and then record number of individuals present after each unit of time has passed.

Case 1 :- Progeny are produced, but not getting added to existing population.

This type of group, where you only track a single group over time, not adding any others, is known as a cohort.

Cohort life table of Phlox drummondii

Start \rightarrow 996 individuals

Class	Age in days	Number surviving
1	0 - 299	996
2	299 - 306	158
3	306 - 313	184
4	313 - 320	151
5	320 - 327	147
6	327 - 334	136
7	334 - 341	105
8	341 - 348	74
9	348 - 355	22
10	355 - 362	0

cohort life table will forever reduce as we don't count seeds produced

The average number of seeds will ~~forever~~ not monotonically increase or decrease.

$R_0 \rightarrow$ Net per capita reproductive rate

$I_x \rightarrow$ Proportion surviving to a particular time interval

$m_{xj} \rightarrow$ Avg. no. of seeds per individual j during each individual

$$\text{Thus, } R_0 = \sum I_x m_x$$

if $R_0 = 1$, each individual replaces itself (stable)

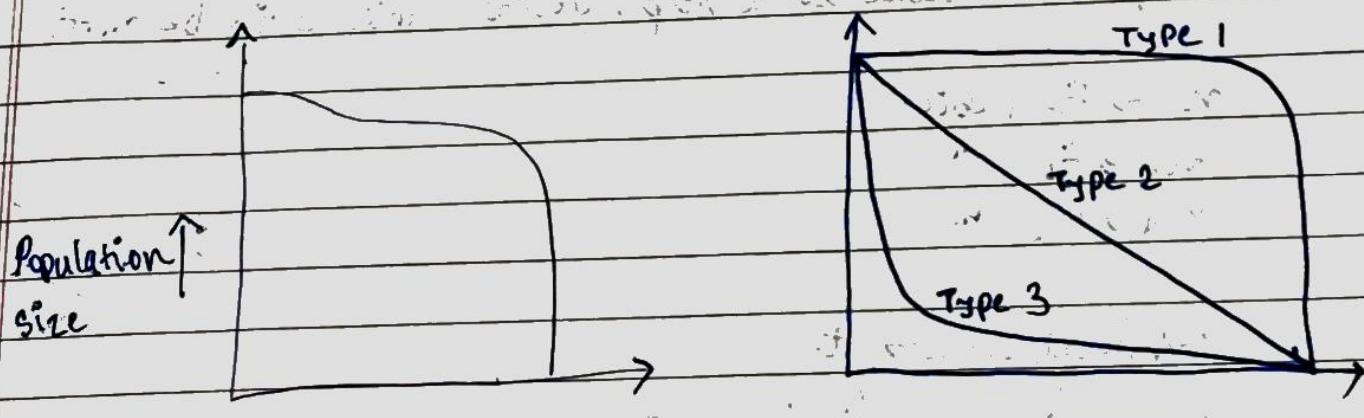
$R_0 < 1$, population will decline

$R_0 > 1$, " " grow

Survivorship Curves:-

Age plotted on x-axis, Number surviving on y-axis (log)

for ph. diatomoides, all are anti-correlated



Time elapsed →

In type 1 → mortality rates low until later in life.

Type 2 → mortality rates are constant.

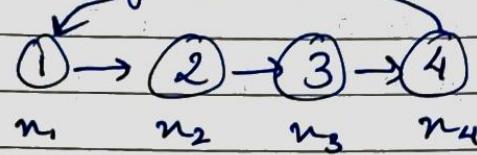
Type 3 → Juvenile mortality rate is high.

These curves are mainly idealizations.

PART-2 :-

Now, we will also consider the babies in the population.

Assume 4 age classes:-



$n_i \rightarrow$ number of individuals in age class i .

$$\text{or } n_1 \times P_1 \rightarrow n_2$$

Fraction which survive

$$n_2 \times P_2 \rightarrow n_3$$

$$n_3 \times P_3 \rightarrow n_4$$

Assume each age class also produces babies.

All babies will be added to n_1 .

Assume the n_1 babies produce F_1 babies.

Thus, in the next time step, total babies will be $n_1 + F_1$.

$$n_2 \rightarrow F_2 \text{ babies}$$

$$n_3 \rightarrow F_3 \text{ "}$$

$$n_4 \rightarrow F_4 \text{ "}$$

Original time $\rightarrow t$

each unit of time increases +1

$$\therefore n_2(t+1) = (n_1(t)) \times P_1$$

$$n_3(t+1) = n_2(t) \cdot P_2$$

$$n_4(t+1) = n_3(t) \cdot P_3$$

$$n_1(t+1) = n_1(t)F_1 + n_2(t)F_2 + n_3(t)F_3 + n_4(t)F_4$$

This computation becomes more tedious with 40-50 age classes.

We use Leslie Matrix :-

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{bmatrix} = \underbrace{\begin{bmatrix} F_1 & F_2 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{bmatrix}}_{\text{Transition Matrix}} \times \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ (n_4)(t) \end{bmatrix}$$

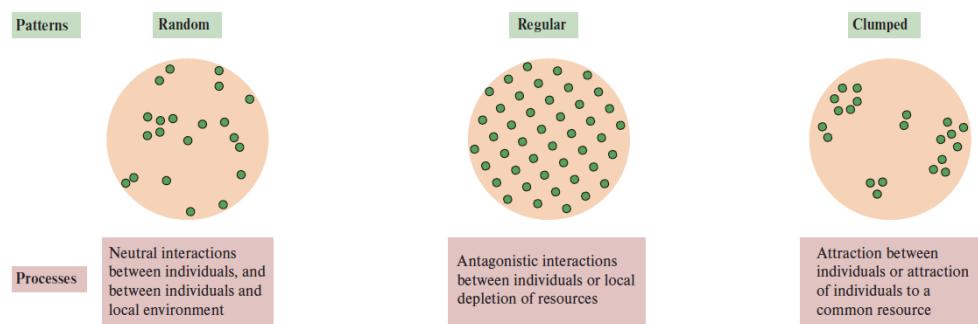
3 Unstructured Models

ECOLOGY AND EVOLUTION

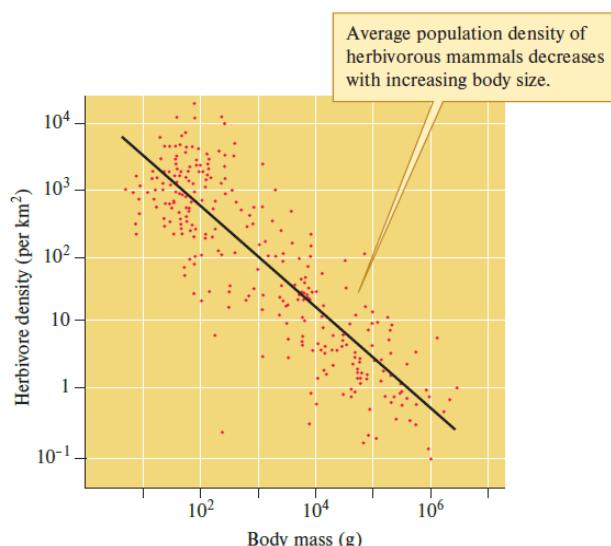
CHAPTER 3 (Lectures + Readings)

UNSTRUCTURED MODELS (population ecology)

- A population is a group of individuals of a single species inhabiting a specific area.
- Environment inhibits the local distribution of the species. The environmental limits of a species are related to its **niche**. Hutchinson defined the “niche” as an **n-dimensional hyper volume**, where n equals the number of environmental factors important for the survival of the species.
This is the **fundamental niche** of the species. The fundamental niche defines the physical conditions under which a species might live in, in the absence of interactions from other species. Whereas, **realized niche** is the actual niche of the species whose distribution is limited by biotic interactions such as competition, disease, parasitism etc.
- **Competition** is the result of overlapping niches of two species.
- In the maps of distribution of the species, three basic patterns of distribution are observed on small scales; random, regular or clumped. On large scales individuals within a population are clumped.
 - A **Random distribution** is one in which individuals of population have an equal chance of living anywhere within an area
 - **Regular distribution** is one when individuals are uniformly spaced.
 - **Clumped distribution** is one where individuals have higher probability of being found in some areas than others.



- The patterns created by social interactions may be reinforced or damped by the structure of the environment. Ex: An environment with patchy distribution of nutrients, nesting sites, water fosters clumped distribution patterns and the one with uniform distribution of resources fosters regular or random distribution patterns.
- Population density **declines** with increase in organism size.



Overall, average population density decreases with increasing body size across a wide spectrum of animal groups.

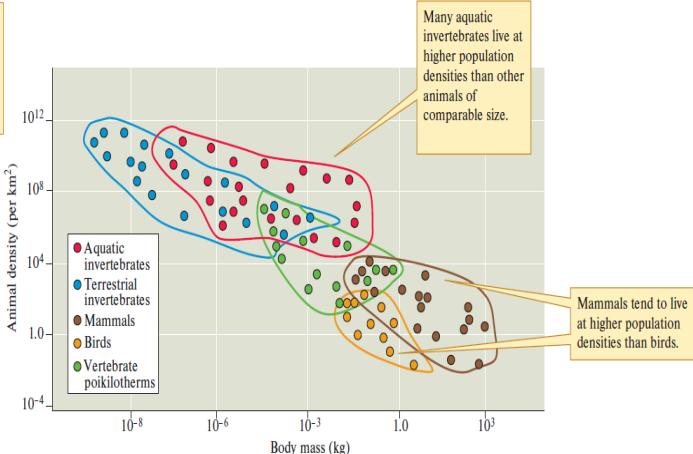


Figure 9.20 Animal size and population density (data from Peters and Wassenberg 1983).

As in animals, plant population density decreases with increasing plant size across a wide range of plant growth forms.

Duckweed, *Lemna*, one of the smallest flowering plants, lives at very high population densities.

The coastal redwood, *Sequoia sempervirens*, one of the largest trees, lives at one of the lowest population densities.

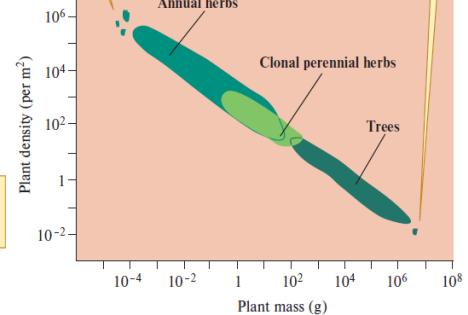


Figure 9.21 Plant size and population density (data from White 1985).

- **Mechanistic models** - A mechanistic model assumes that a complex system can be understood by examining the workings of its individual parts and the manner in which they are coupled.
- **Phenomenological models** - A phenomenological model is a scientific model that describes the empirical relationship of phenomena to each other, in a way which is consistent with fundamental theory, but is not directly derived from theory. In other words, a phenomenological model is not derived from first principles.

- First Law of Population Dynamics:

$$N_{t+1} = N_t + N_t (B + I - D - E)$$

where, B = number of births within the interval t to t+1

I = number of immigrants to the population during the interval

D = number of deaths within the interval t to t+1

E = number of individuals that have emigrated during the interval

(B, I, D, E are per capita rates)

- $N_{t+1} = N_t + N_t (y')$
- $N_{t+1} = N_t (1 + y')$
- $N_{t+1} = N_t (y)$

where $y = \lambda = 1 + y'$

$$N_1 = y N_0, N_2 = y^2 N_0$$

$$\text{So, } N_t = y^t N_0$$

- This law gives the behavior of a population in the absence of any external influence. This was for the discrete time version; the continuous time analog would look like-

$$\frac{dN}{dt} = rN$$

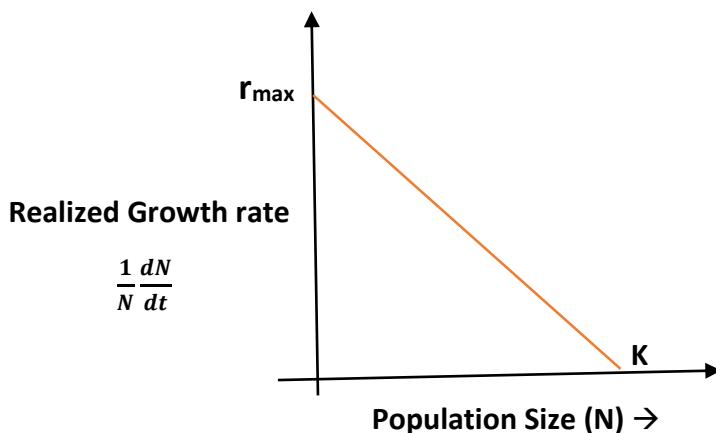
i.e., per-capita growth rate is a constant
solving it gives;

- $N_t = N_0 e^{rt}$
- $y = e^r$

where r is the **per-capita rate of increase**

This is for the density independent populations

- Refining the model: Plugging in Density dependence and assuming it comes down linearly
(As population size increases, the amount of resources available starts to decline hence affecting the growth rate of the population- Density dependence)



- The rate at which a population increases in size if there are no density-dependent forces regulating the population is known as the *intrinsic rate of increase* – r_{\max} . This is a theoretical concept. The actual or realized per capita rate of increase is generally less than r_{\max} , as natural populations are subjected to factors such as disease, competition etc.

The equation of the straight line gives-

$$\frac{1}{N} \frac{dN}{dt} = r - N \frac{r}{K}$$

$$\frac{dN}{dt} = rN(1 - \frac{N}{K})$$

This is the continuous logistic equation or the Verhulst- Pearl Equation.

For discrete logistic equation-

$$(N_{t+1} - N_t) / N_t = r (1 - N_t / K)$$

- $N_{t+1} = N_t (1 + r (1 - N_t / K))$

If one considers population growth rate ($\lambda = N_{t+1}/N_t$) instead of per capita growth rate

- $\lambda = r N_t (1 - N_t / K)$

Dividing both sides by K -

- $X_{t+1} = r X_t (1 - X_t)$

- In many cases growth rate doesn't fall linearly but falls in a negative exponent. So y axis is changed to

$$\ln(N_{t+1}/N_t) = r (1 - N_t / K)$$

- $N_{t+1} = N_t e^{r(1 - N_t / K)}$

(This is called the exponential logistic/ Ricker/ Discrete logistic model)

-----Populus for simulations-----

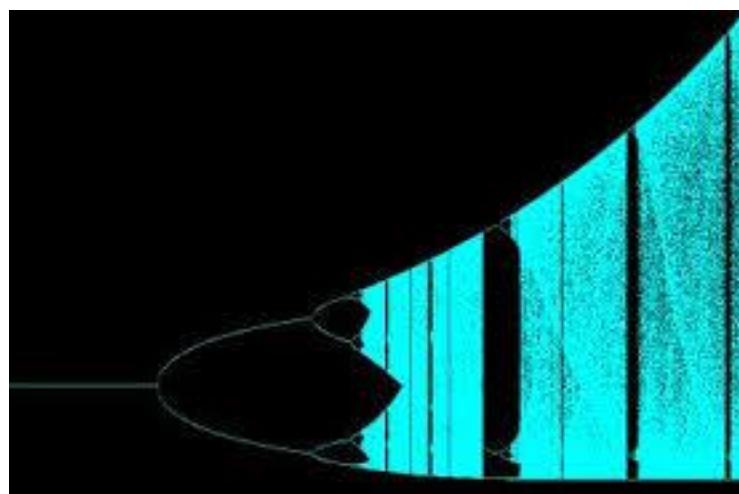
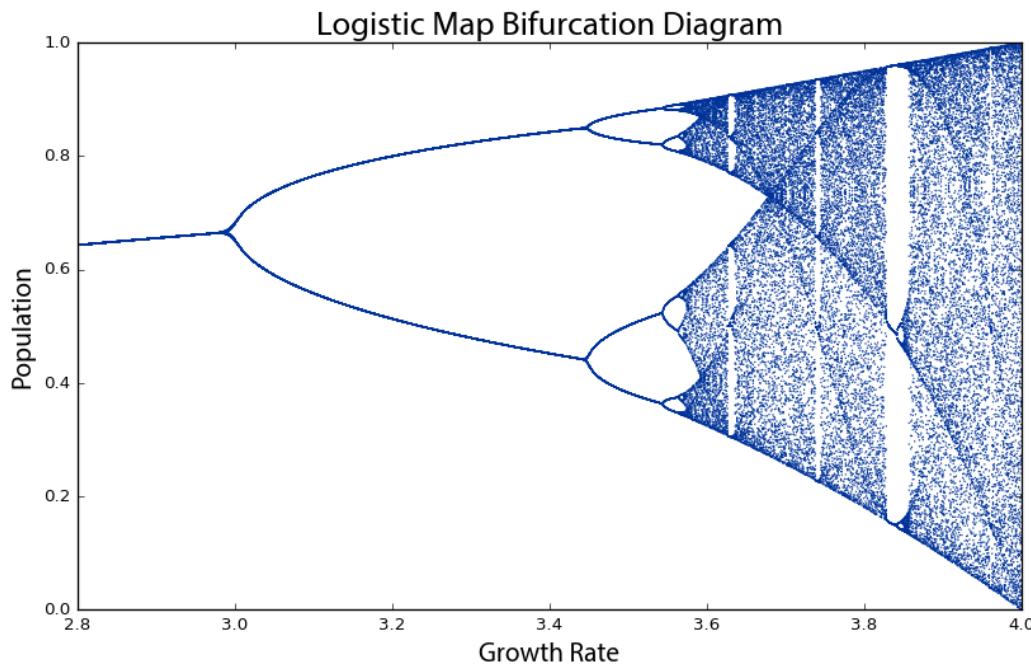
- By increasing value of r stable point equilibrium gives rise to a two-point cycle then to a 4-point cycle, then 8-point cycle and after a point all periodicity disappears.

Iterating a deterministic model and getting a completely stochastic trajectory is called Deterministic Chaos.

BIFURCATION DIAGRAM (plotting N_t vs r)

https://www.youtube.com/watch?v=VjzkW1lVI4&ab_channel=MichaelHoggUK

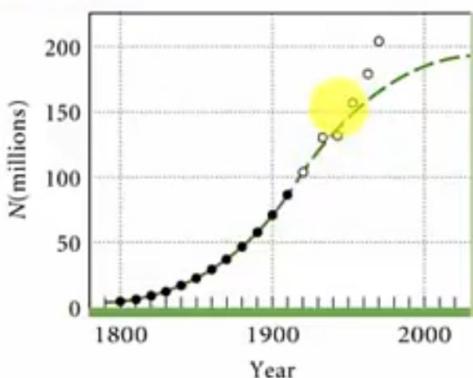
https://www.youtube.com/watch?v=nxcKh36rep0&ab_channel=-math134



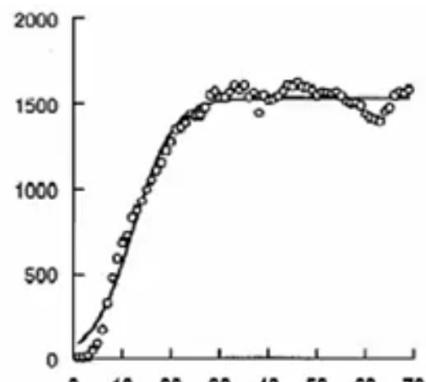
Bifurcation diagram for Ricker Model

- A chaotic trajectory by its own definition can never repeat itself. **thus in a bifurcation diagram it looks like a complete smear**

- Continuous logistic curves are seen in populations in real world. The model does a pretty decent job in fitting experimental data.



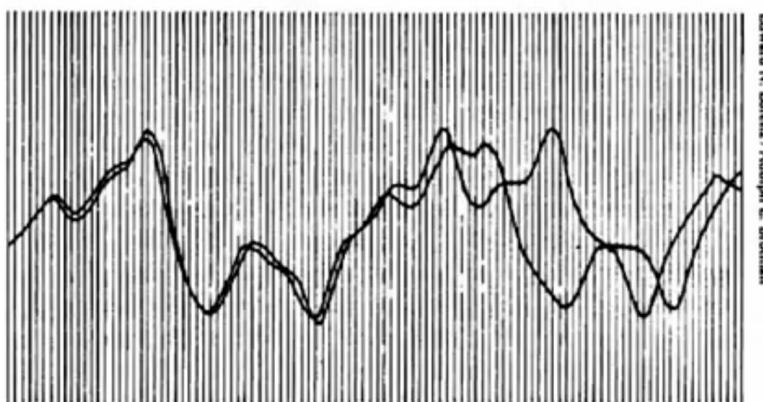
Human population size in USA
Pearl & Reed 1920



Population dynamics of the rotifer
Brachionus plicatilis

Yoshinaga et al, 2001

Edward Lorentz and the Weather patterns



Edward N. Lorenz / Adolph E. Brodman

HOW TWO WEATHER PATTERNS DIVERGE. From nearly the same starting point, Edward Lorenz saw his computer weather produce patterns that grew farther and farther apart until all resemblance disappeared. (From Lorenz's 1961 printouts.)

- Edward N. Lorenz - Two systems with trajectories starting arbitrarily close to each other end up diverging after some time. This is called **Sensitive Dependence to Initial conditions** or **Butterfly Effect**.
- Robert published review papers on these in Nature.
These papers suggested that simple models can lead to very complicated dynamics and thus the hope that what looks like ultra-complex dynamics might be arising out of very simple equations after all. Thus began the era of finding chaos in pretty much every linear system that one cared to look at.
- There are two methods one can apply to study these chaotic systems:

1) Estimate the Lyapunov exponent from the time series data

Lyapunov exponent of a dynamic system is a quantity that characterizes the rate of separation of infinitesimally close trajectories. Quantitatively two trajectories in phase space with initial separation vector δZ_0 diverge at a rate given by

$$|\delta Z(t)| \approx e^{\lambda t} |\delta Z_0|$$

where λ is the Lyapunov exponent

REMARKS - This method requires very long time series which are possible to obtain for physical systems, **but not for biological systems**

Other models were later developed in estimating the Lyapunov exponent better; but still requirement of data came down from thousands to hundreds (which still was difficult to get in biological populations)

- 2) **Find Parameter estimates by fitting models to real time series data** and hence characterize the populations as 2 point cycles, 4 point cycles, chaos or damping.

Pros- can work for short noisy data sets.

Cons- One must assume that the real model is known

- Fitting models sometimes is more an art than a science

The Hassel Model

$$N_{t+1} = \lambda N_t (1 + a N_t)^{-\beta}$$

where

N_t is the population size at time t

λ is the growth rate parameter

a and β are parameters regulating the density-dependent feedback term

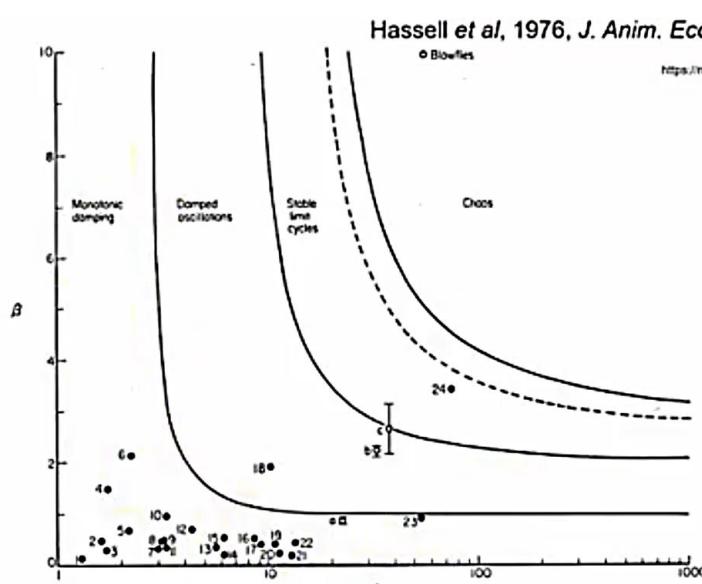
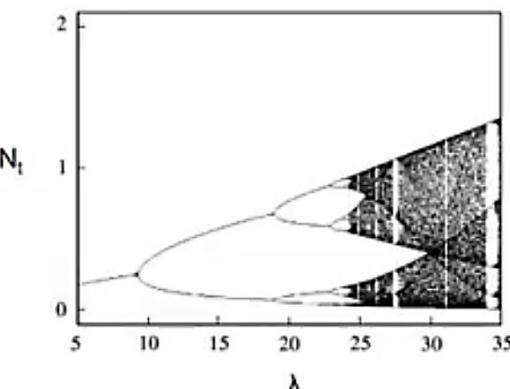
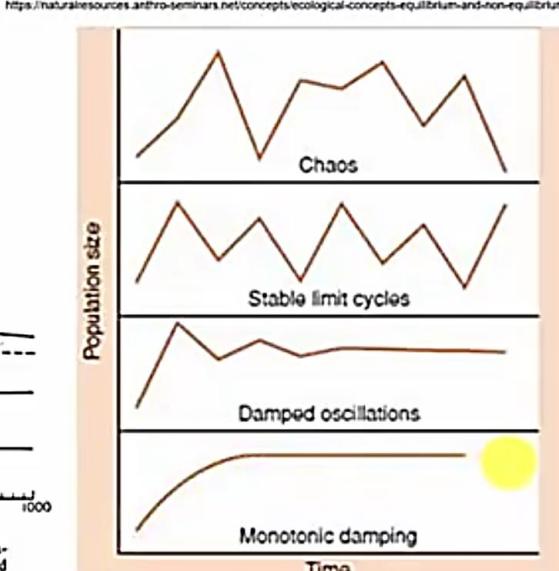


FIG. 2. Stability boundaries between the density dependent parameter, β , and the population growth rate, λ , from eqn (1). The solid lines separate the regions of monotonic and oscillatory damping, stable limit cycles and chaos. The broken line indicates where two-point limit cycles give way to higher order cycles. The solid circles come from the analyses of the life table data in Table I and the number by each point refers to this table. The hollow circles are discussed under 'Laboratory experiments'.

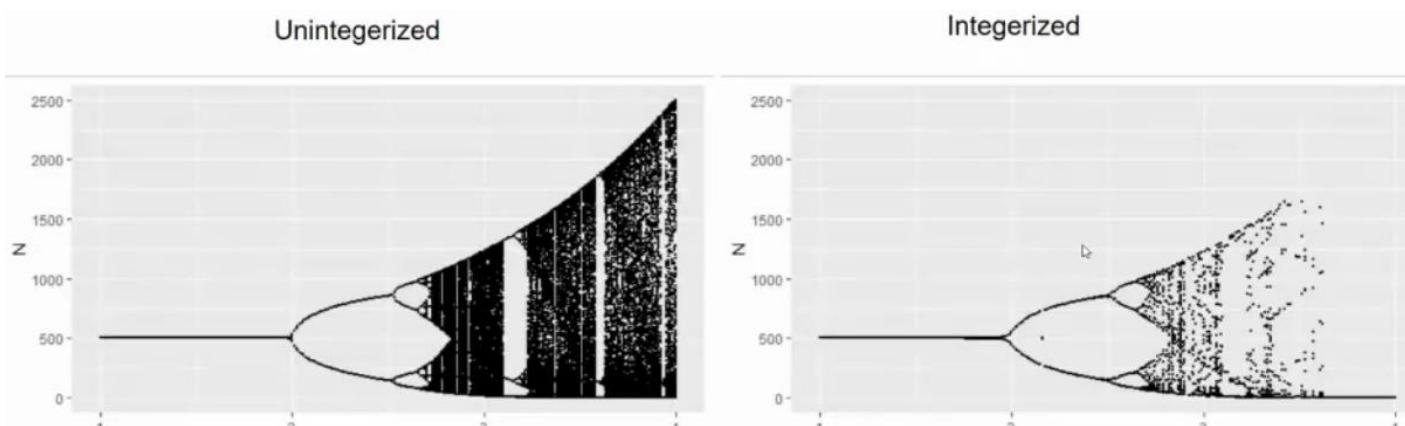


- 24 different populations were studied. 22 populations out of 24 showed monotonically decreasing, 1 population showed chaos, one damped oscillations and one in between damped oscillations and stable limit cycles, implying most natural populations are exhibiting relatively simple dynamics.
- **Why is it we are unable to see chaos in real systems???**

- Most simple models of population dynamics predict that populations could, in principle, exhibit a variety of dynamic behaviors ranging from stable dynamics to limit cycles to chaos (May, Nature, 1976). This led to a large number of empirical studies that tried to document chaos in real, biological populations.
- Hassel et al demonstrates that most populations actually exhibit very simple behavior, which intuitively did not make sense.

Solution: **Real population sizes are always in integers**; most model outputs are never so. So, Integerizing our population sizes in models would solve this issue.

INDIVISIBILITY OF ORGANISMS – LATTICE EFFECT



Observations from the Lattice Effect

- In the unintegerized model, one can never get an extinction in a population. (Because $e^0 = 1$)

$$(\text{Ricker Model- } N_{(t+1)} = N_{(t)} e^{r[1 - (N(t)/K)]})$$

The integerized version shows that at high values of r , extinctions are coming in.

- A characteristic feature of chaotic system is that it never repeats itself, thus in a bifurcation diagram it looks like a complete smear. Those smears have disappeared in the integerized models. (Chaos disappears)

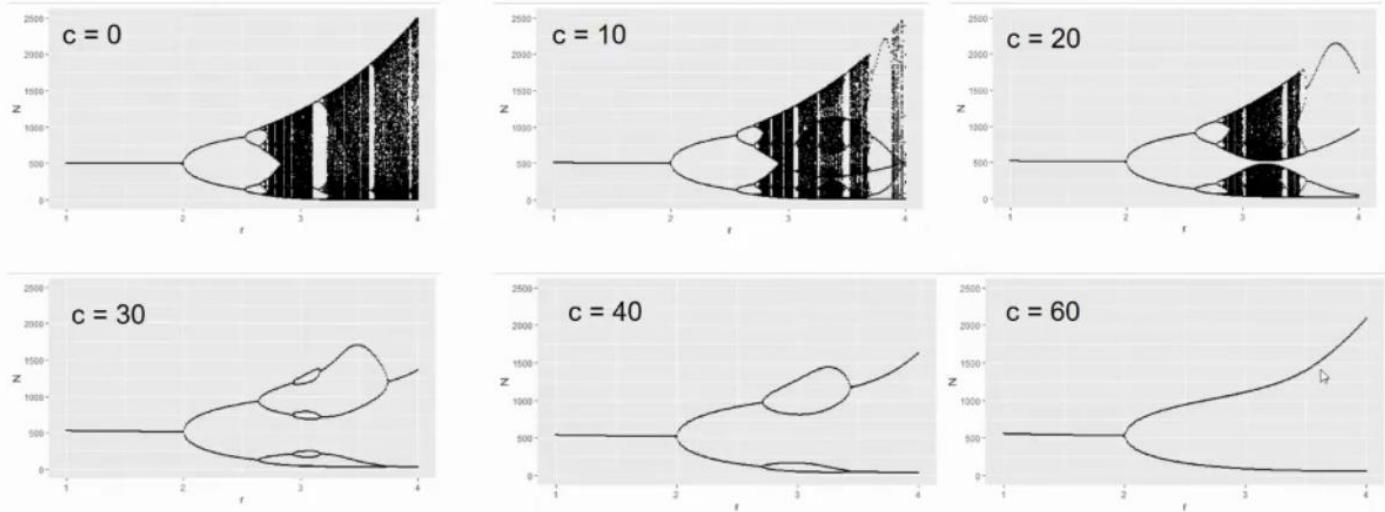
Inference

- Chaos implies that the points in a time series never repeat themselves. But integerization coupled with upper bound on population size imposed by the model structure, **makes the set of possible values that the system can take, finite**. In other words, sooner or later, a particular value has to repeat and that is the point where periodicity sets in.
- The lattice effect **does not exclude the possibility of limit cycles with long periodicities**.

Effects of constant immigration

$$N_{t+1} = f(N_t) + c$$

$$F() = \text{Ricker}, K = 500, N_0 = 10$$



This is called **pinning**.

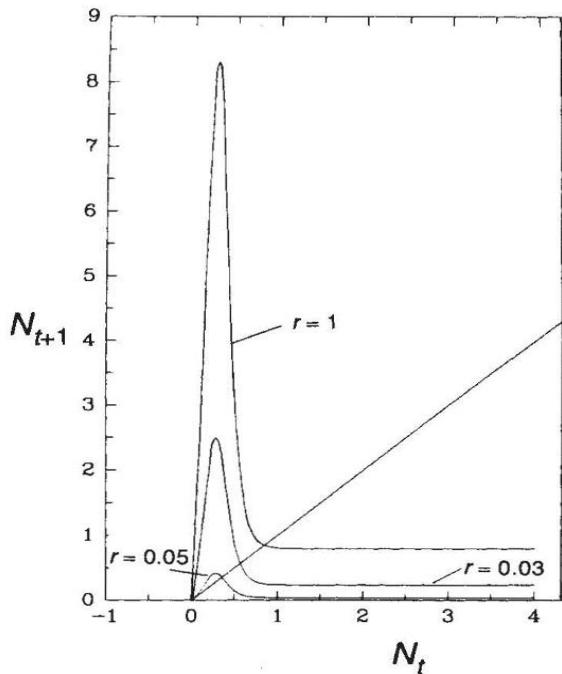
- As constant immigration increases, chaos disappears

Reasoning- By adding a constant value (c) to the equation at every time-step, we are shifting the return map upward by ' c .' This will push the point of intersection of $y=x$ towards the "tail" of the graph. Since the point is basically a stable point, by pushing the slope of the graph at the point closer to 0 (i.e. between -45 and +45 degrees), we can see the system becoming more and more stable. This is for smaller values of r . For larger values, we can do the same thing but the graph would be N_t (population size at time-step t) vs N_{t+2} for 2 point-cycle, N_{t+4} for 4-point cycle and so on (because the values will start repeating only after iterating the given number of times).

Period Doubling Reversal – Levi Stone

$$N_{t+1} = N_t e^{r(K - N_t)} + \lambda$$

without loss of generality let $K=1$



F has a plateau region that flattens out for large N_t . The plateau can occur whenever there is a point of inflection or if the second derivative F'' suddenly changes sign to the right of the critical point.

N^* is the fixed point at the intersection between the line $N_{t+1} = N_t$ and the curve $F(N_t)$. The stability of N^* is ensured if the slope $S(N) = r F'(N)$ of the curve at the intersection point satisfies $|S(N^*)| < 1$.

Increasing r serves to reduce $S(N^*)$, until $S(N^*) = (-1)$, when a period doubling bifurcation occurs, the fixed point N^* becomes unstable and a stable 2 cycle is born. A succession of period doublings follow in the usual manner as r gradually increases.

When r is large, the equilibrium point $N=N^*$ is stable because it lies in plateau region where $S(N^*) \approx 0$

The existence of single stable point depends on the concavity and height of the plateau.

- The breakdown of period doubling occurs when for some stable k- cycle, the slope of the k-fold map $F^k(N_i)$ is constrained so that $S(N_i) = r^k F^k(N_i) > (-1)$ and a period doubling bifurcation cannot take place. For similar reasons, perturbations that serve to translate the plateau vertically upwards yields the same qualitative result.

Model Complexity, Turchin and Taylor - 1992

- They took a larger number of time series with different time lags and varying complexities, and instead of using mechanistic models like Ricker or Logistic, they fitted polynomials. One can fit any trajectory by having a sufficiently complex polynomial of sufficiently higher degree.

The underlying question being "**Is $N_{(t+1)}$ a function of $N_{(t)}$ alone?**"

- They also put in a penalty function. They used Akaike Information Criterion (AIC), an estimator of in-sample prediction error and thereby relative quality of statistical models for a given set of data. In-sample prediction error is the expected error in predicting the resampled response to a training sample. Given a collection of models for the data, AIC estimates the quality of each model, relative to each of the other models. Thus, AIC provides a means for **model selection**.
- Finally, they came up with a suit of models for each time series and found optimal models out of those for each dataset. From the models, they extracted the parameter values for each time series and tried to figure out the dynamics of the population.
- All kinds of behavior including exponential damping, oscillatory damping, limit cycles and chaos were observed.

CONCLUSION-

- Use of overly simple models for reconstructing endogenous dynamics from data may be biased in favor of finding stability. This disproved Hassel's theory of most populations having very simpler dynamics.

Controlling the dynamics of real populations

- **Problems-**
 - Poor knowledge of the real system and no access to the system parameters.
 - Short and noisy time series, difficult to distinguish between different dynamics
 - Biological systems are inherently noisy and extinction prone.
- **Theoretical approaches:**
 - Perturb state variables rather than parameters
 - Concentrate on measurable and biologically relevant indices of stability like constancy and persistence

Case Study

Does pinning really work? - Suthirth Dey

Local perturbations do not affect stability of Laboratory fruit fly Metapopulations.

It didn't really work although simulations suggested that it should.

Major findings- Sub population extinctions reduce the impact of pinning on local (and hence global) stability.

AIM-

- A) Devise a method for stabilizing the dynamics of populations (spatially homogeneous and explicit) which will be:
 - a) Implementable in a real population
 - a) Robust to noise and realistic extinction probabilities
 - a) Will be applicable in a biologically meaningful parameter range

B) Empirically validate the proposed method

The best candidate: Limiter control*
Do not allow the population size to go above / below a certain threshold value.

Problem: How does one define the threshold for different kinds of organisms with different equilibrium population sizes?

Possible solution: Make the control dependent on the population size.

Adaptive Limiter Control (ALC)

$$N_{t+1} = f(N_t) \dots \dots \dots \text{ if } N_t \geq c.N_{t-1}, \\ N_{t+1} = f(c.N_{t-1}) \dots \dots \dots \text{ if } N_t < c.N_{t-1}$$

Biological interpretation:

Do not allow the population to go below a fraction c of the size of its previous generation.

Trivial stability if $c = 1$, we are interested in lower values of c .

Modeling the dynamics: Ricker Model

$$n_{t+1} = n_t \exp(r(1 - n_t/k))$$

n_t = Population size at generation t

r = Growth rate

K = Population carrying capacity

Why use the Ricker model?

- Simple generic model with no species specific parameters
- Derived analytically from first principles based on biological assumptions
- Empirically shown to be widely applicable

Quantifying Stability-

Constancy:

Stability = Reduction in amplitude of fluctuation in time series

Fluctuation Index,

$$FI = \frac{1}{T\bar{N}} \sum_{t=0}^{T-1} \text{abs}(N_{t+1} - N_t)$$

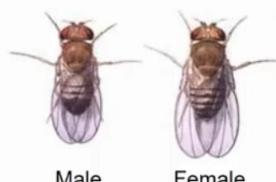
Persistence:

Stability = Reducing the frequency of extinctions within a given time period.

• Economic cost: $\text{Effort magnitude} = \left(1/\left(T \times \bar{N}\right)\right) \times \sum_{t=1}^T |B_t - A_t|$

• Effective population size: $N_e = T / \sum_{t=1}^T 1/N_t$

Experiment using *Drosophila melanogaster*



Drosophila melanogaster

Three treatments

$c = 0$ (Ctrl),

0.25 (LALC)

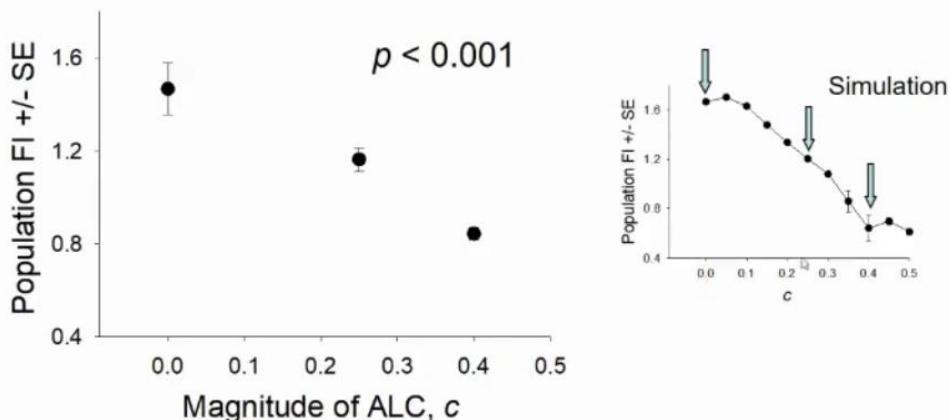
0.4 (HALC)



Single-vial *Drosophila* pop.
Census data over 13 generations

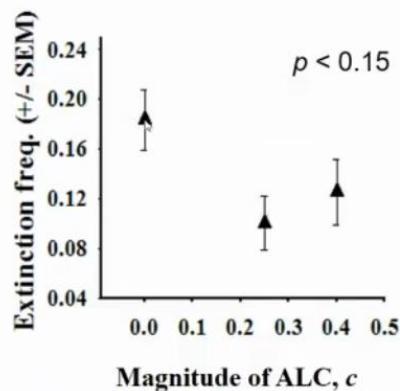
8 replicate populations per treatment

Experiment: Effect of ALC on constancy stability



ALC significantly enhances constancy stability of experimental populations.

Experiment: Effect of ALC on persistence stability



Even a low value of ALC enhances persistence of experimental populations, although the difference is not significant at the 5% level.

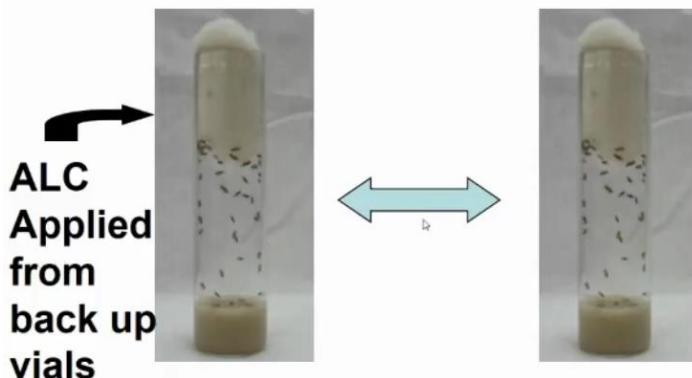
Result -ALC can stabilize the dynamics of real spatially unstructured populations.

Metapopulations- A metapopulation is a group of populations that are separated by space but consist of the same species. These spatially separated populations interact as individual members move from one population to another.

- Migration rates affect Metapopulation constancy.



Experiment on two-patch metapopulations



Two-patch *Drosophila* metapopulation

8 replicate metapopulations

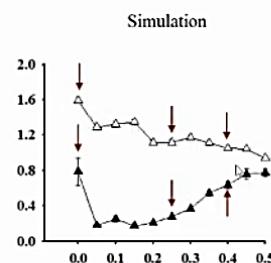
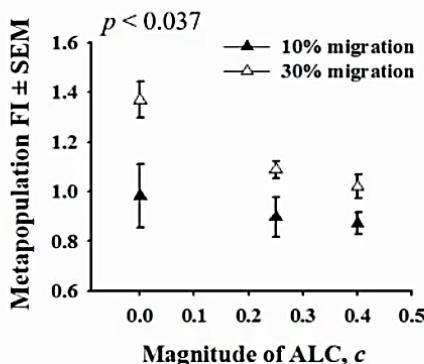
Rate of migration: 10% or 30%

Three values of c : 0, 0.25, 0.4

Census data over 15 generations



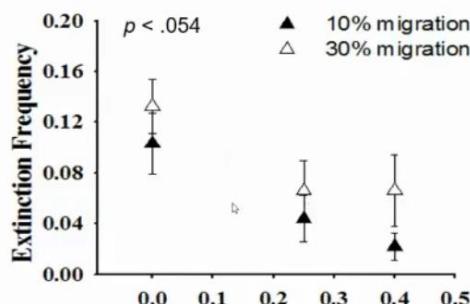
Experiment: Effect of ALC on metapopulation constancy



ALC significantly reduces metapopulation FI under high but not low migration.
No migration \times ALC interaction.

- ALC enhances constancy of unstable Metapopulations, but does not affect the stable ones.

Experiment: Effect of ALC on persistence



ALC promotes persistence under both migration rates,
perhaps by slightly different mechanisms

- ALC is a potent mechanism for enhancing constancy and persistence in real biological populations and Metapopulations.
- Since, the empirical results are supported by simulations on a host of non-drosophila specific models, the method is likely to be broadly applicable.
- This was the first control method empirically shown to work for a biological population.
- The method reduces both population fluctuations as well as extinction probability.
- The result is generalizable in populations with other rates/kinds of extinction, other values of K, other rates of migration and different number of subpopulations.
- Daniel Franco Leis and Frank M. Hilker mathematically established why ALC attains stability in single populations and they also proposed other adaptive limiter variants.
- Thus, ALC enhances constancy and persistence, is robust to many biological realities, works for real single as well as Metapopulations and has a mathematical explanation also for how it works. Hence, this was one of the most studied algorithms in population dynamic literature.

Comparing the efficiency of control methods: the problem and a solution

The problem

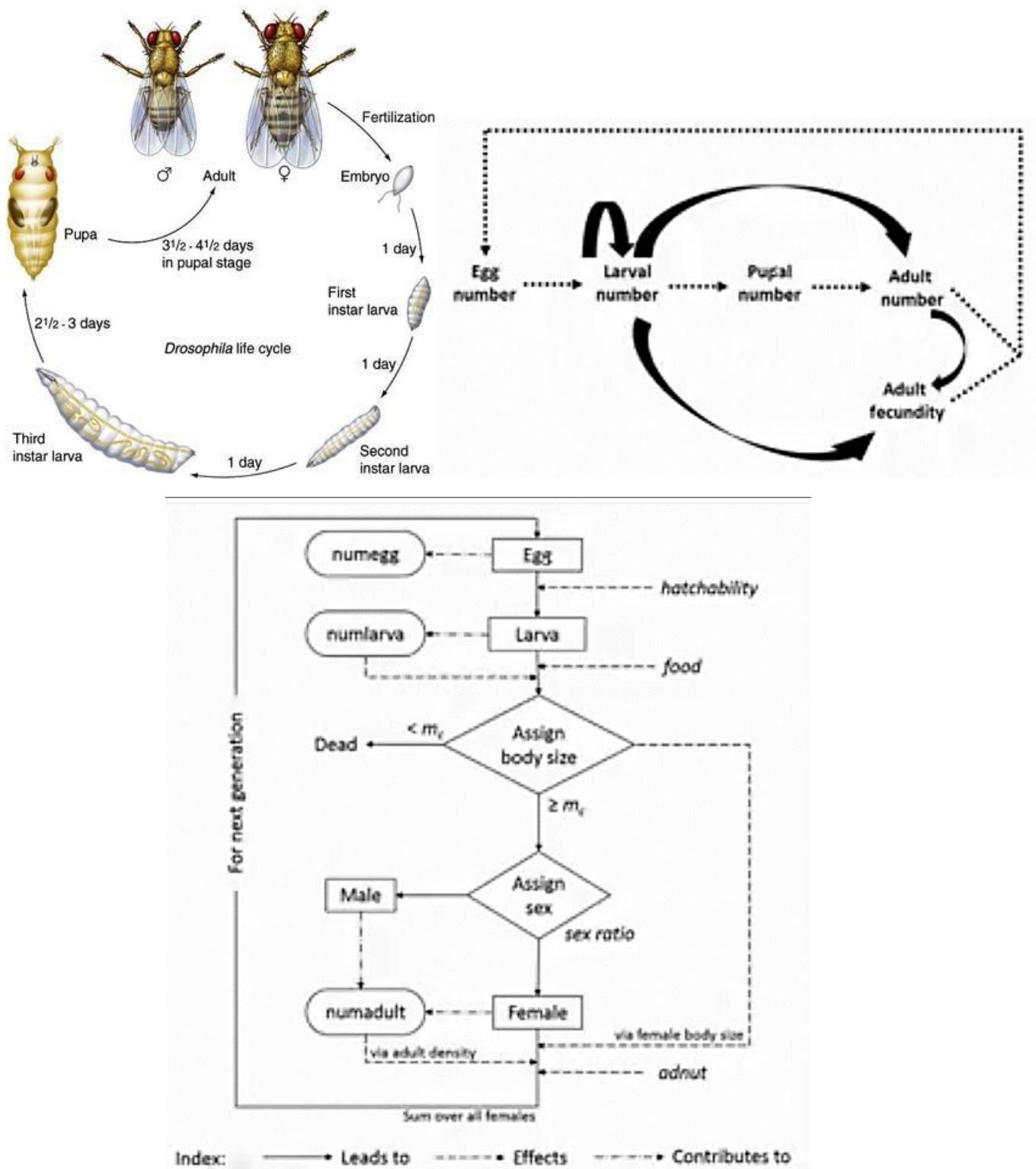
- Different models, model parameters and stability concepts
- For large enough control parameter values, most control methods can induce (almost) any level of stability.

One possible solution

- Fix a model and corresponding parameter values
- Fix a particular level of stability (say 50% reduction in FI)
- Figure out the parameter values for each method, at which that level of stability is attained,
- Compare the efficiencies of these methods at those parameter values using other criteria (e.g. economic cost, effective population size etc.)
- Integrate the performance of each method across these multiple axes using some kind of a composite index,
- Compare the control methods using this composite index.

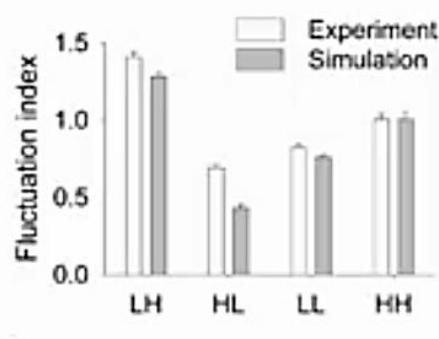
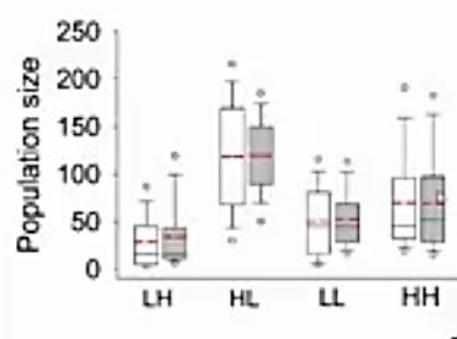
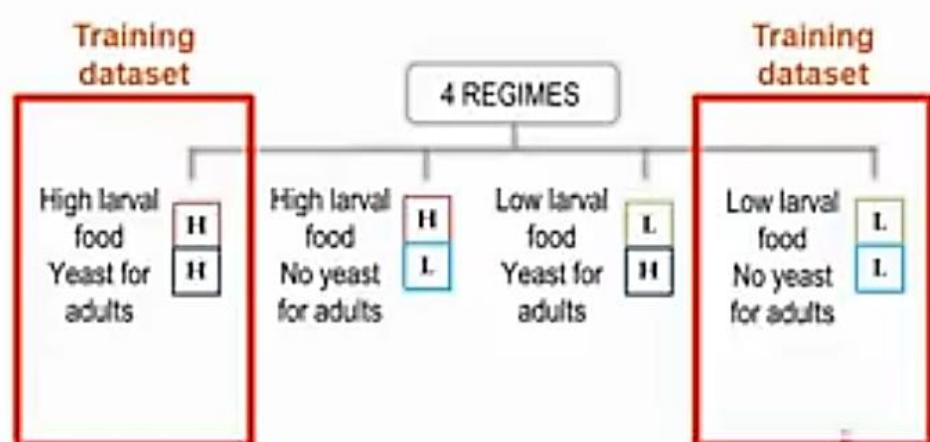
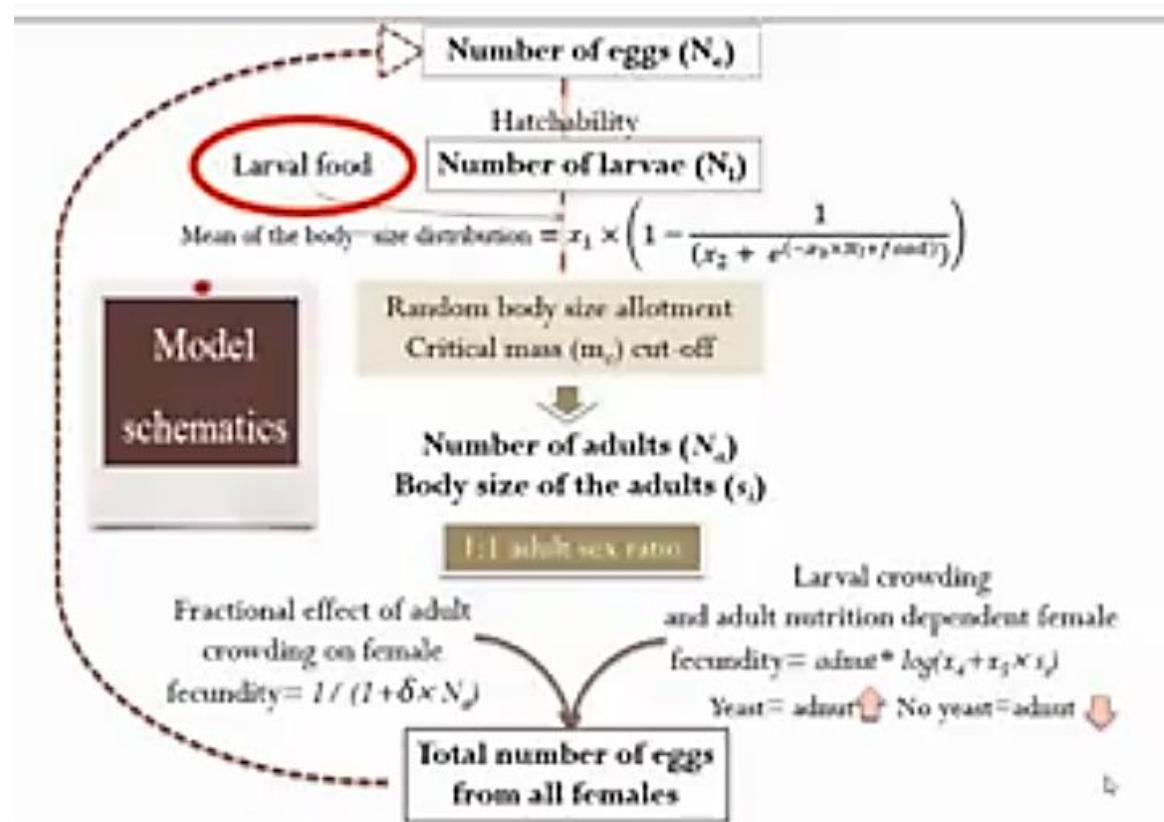
An individual based model for Drosophila dynamics. (3.6)

(interaction of life history traits with nutritional availability to shape population dynamics and population stability)

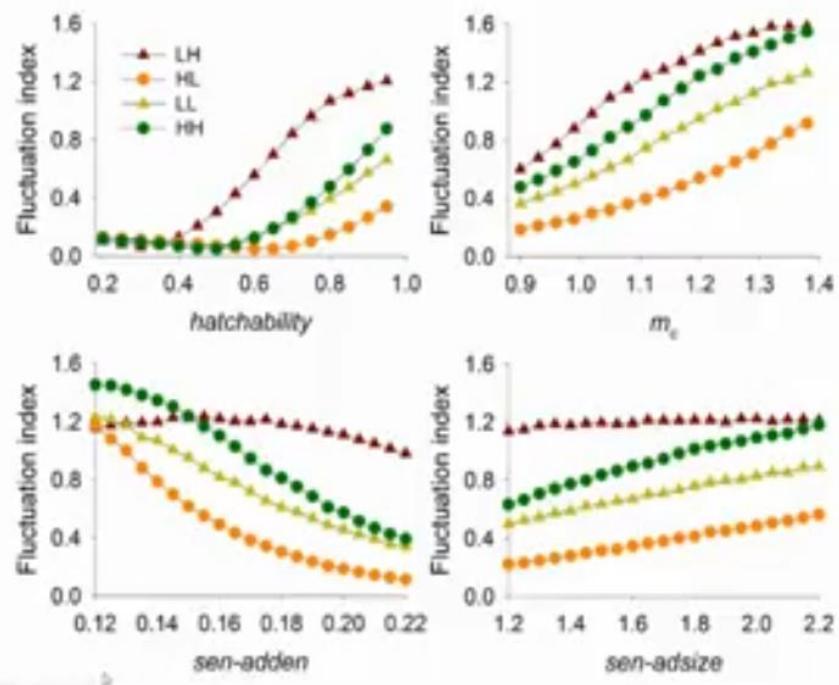


Features of the model-

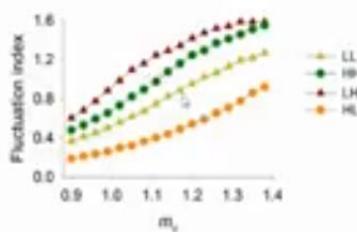
- Stage structured, individual based, discrete generation model.
- Incorporates important life history traits like hatchability, critical mass (m_c), adult body size and fecundity; typical of many holometabolous insects.



Model exploration



Effect of critical mass (m_c) on stability



Model prediction: Irrespective of nutritional conditions, low

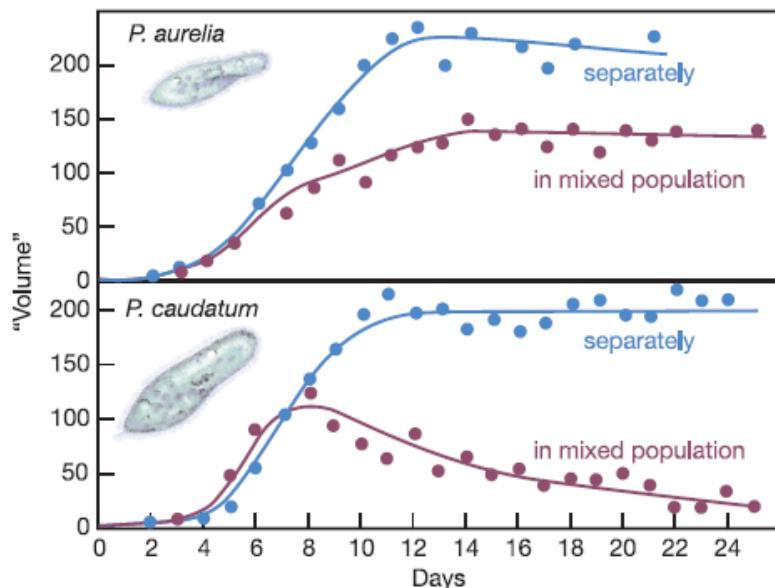
m_c tends to decrease FI and thus increase stability.

CHAPTER 4 (Lectures + Readings)

COMPETITION (community ecology)

Interaction 1- Competition

- **Gauss's Principle of Competitive exclusion-** No two species with the same niche coexist.



Growth of two *paramecium* species separately and in combination.

Source: Gause, Georgyi Frantsevitch. 1934 *The Struggle for Existence*. Dover Publications, 1971 reprint of original text.

- **David Tilman- R* rule in exploitative competition**

When two or more species are limited by the same resource, the species that can maintain positive per capita growth at the lowest resource level will exclude all other species. He studied this in diatoms.

- Limiting resource is not the only condition for competition. Ex- some of the individuals may corner up the resources i.e., limited resources are not necessarily natural, it can be artificial too.
- Any use or defense of a resource by an individual that reduces the availability of resources to other individuals is called competition.
- Two types- **Interspecific** (between members of different species) and **Intraspecific** (among the individuals of same species) competition.
- Density dependent reduction in population growth rate, competition for finding mates are examples of Intraspecific competition
- Features of Interspecific competition-
 - Non-trophic interaction (one species does not eat another)
 - Reduced population growth rate or equilibrium number for both or at least one of the populations.
 - Introducing individuals of different species gives:

$$\frac{dN_1}{dt} = r_1 N_1 [K_1 - N_1 - \alpha_{12} N_2]$$

$$\frac{dN_2}{dt} = r_2 N_2 [K_2 - N_2 - \alpha_{21} N_1]$$

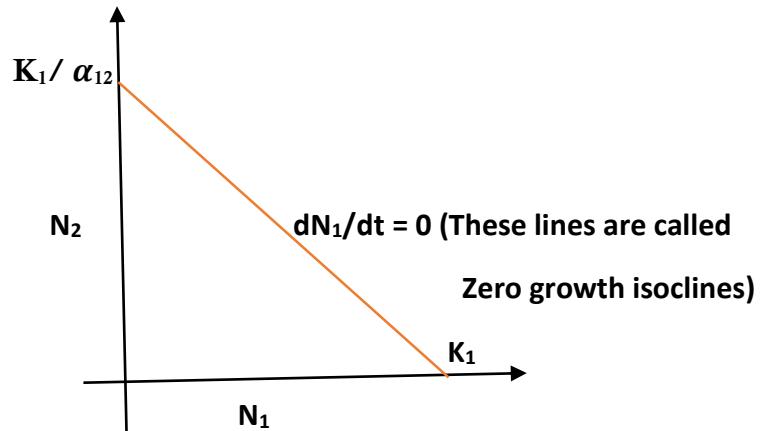
where α_{12} is the interspecific competition coefficient

- This is **Lotka-Volterra competition equation**

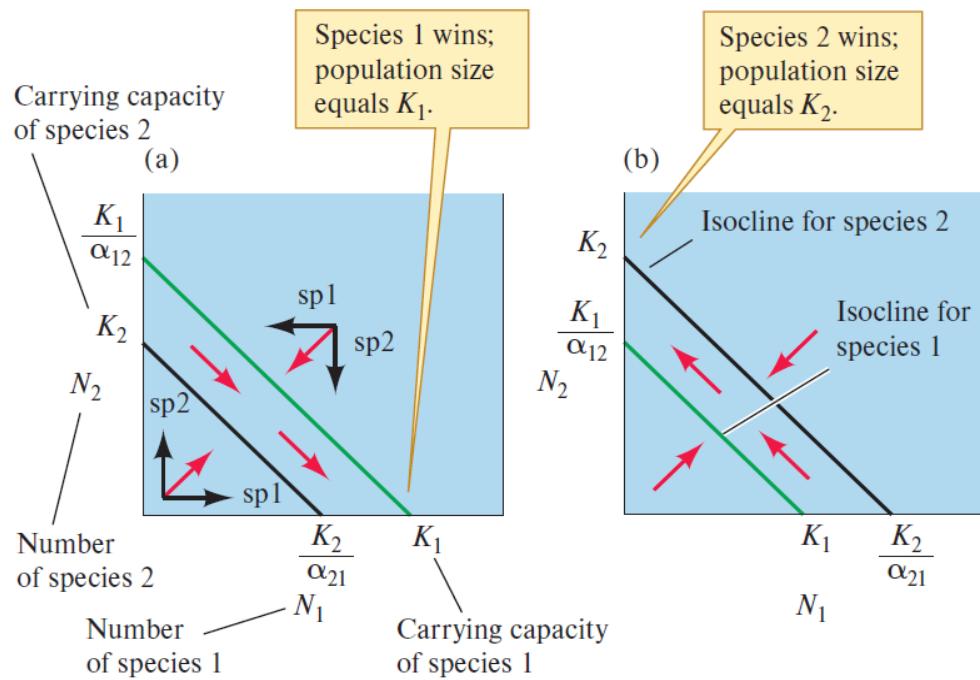
When $\frac{dN_1}{dt} = 0$

$$\Rightarrow K_1 - N_1 - \alpha_{12} N_2 = 0$$

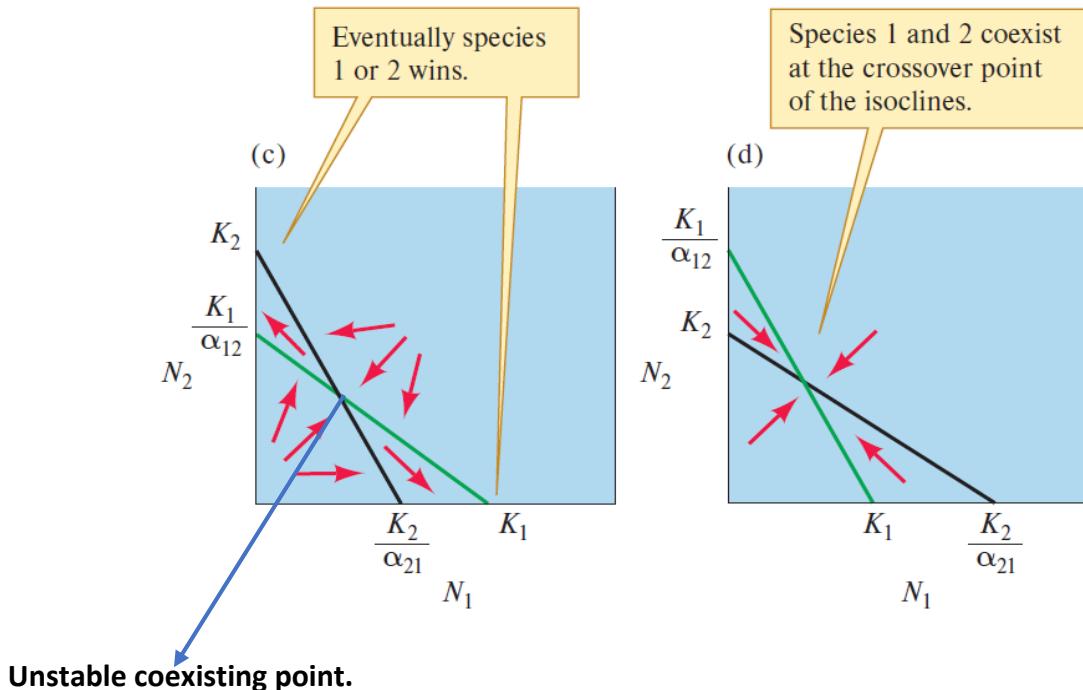
$$\Rightarrow N_2 = 1/\alpha_{12} (K_1 - N_1)$$



All Possible graphs of the isoclines of two species-



Arrows show trajectories of population change in population of species 1 and 2.



The orientation of isoclines for zero population growth and the outcome of competition according to Lotka-Volterra competition model.

- ⇒ **The outcome is independent of changes in r and K**
- ⇒ **Trajectory of the system – refer Populus.**
- ⇒ **If K_1 wins and K_2 goes extinct it can be either due to K-stability or α stability i.e., isocline of species 1 above the isocline of species 2.**

- **Invasion** - sudden introduction of non-native species in an ecosystem.

Example-

- 1) Arapaima, Alligator gar in Kerala,
- 2) *Eichhornia crassipes* (Water hyacinth)- Terror of Bengal

Kottapuram Integrated Development Society (KIDS) – 300 women in Paravur were trained to make crafts out of Water Hyacinth, thereby using them as economic benefit.

- 3) Asian Carps in the Mississippi river basin and northward lakes. They eat away all the plankton, which is the foundation of the food web of the ecosystem.
- 4) *Caulepra taxifolia*

- **Resource- Utilization Niche**- focuses entirely on what members of a specific population in some locality actually do-in particular, how they use resources – by Robert McArthur and Richard Levins.

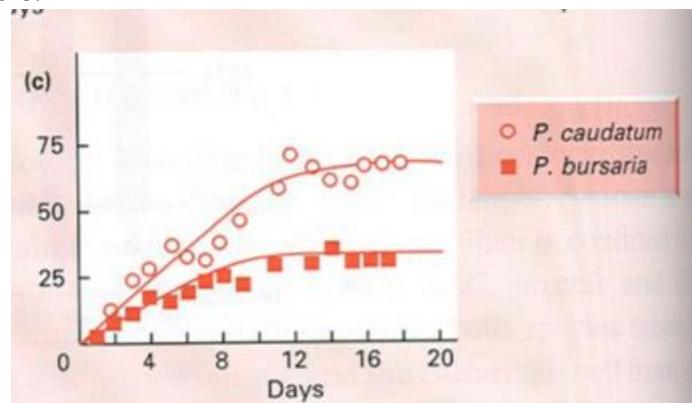
Kind of niche axes typically used for utilizations-

- Habitat (microhabitat, macrohabitat)
- Food type (food size and hardness)
- Time (daily and seasonal activity)

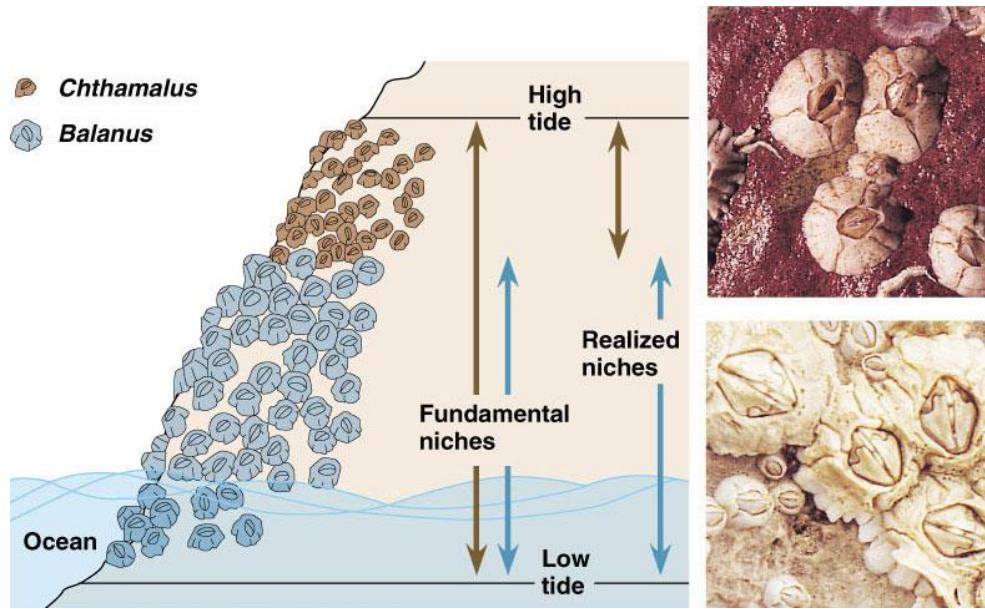
- Coexistence is possible if there is a separation/ partitioning of the niche. Resource partitioning can be spatial, temporal, morphological or conditional niche differentiation

- **Spatial Niche Separation-**

- 1) Both coexist as *P. caudatum* feeds on the top layers of the culture while *P. bursaria* feeds on the bottom layers.



- 2) Cornell's Barnacles-



- Chthamalus are more resistant to defecation over Balanus

- **Temporal Niche Separation-**



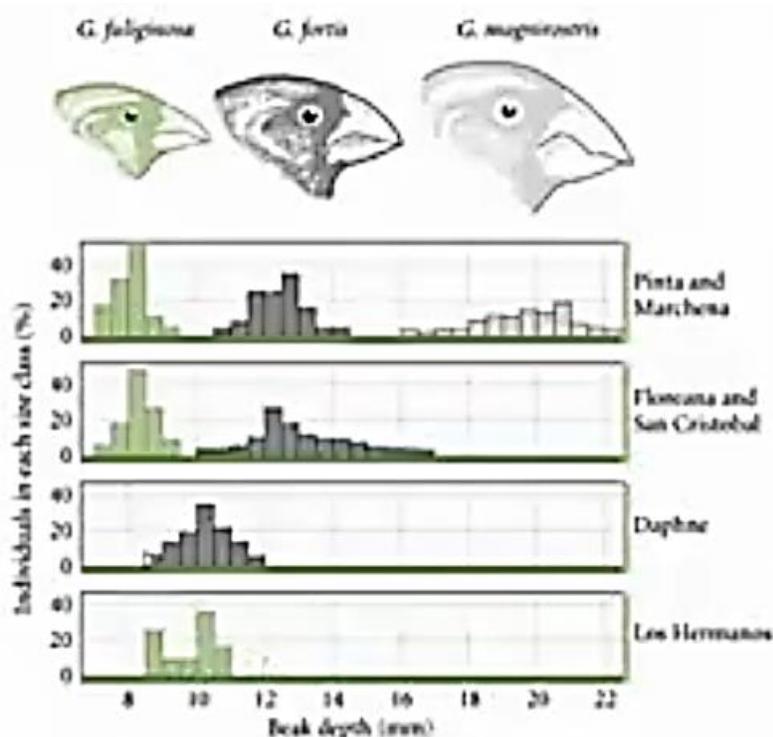
Common spiny mouse
(*Acomys cahirinus*)
Nocturnal

Golden spiny mouse
(*Acomys russatus*)
Diurnal

- These coexist in the deserts of Israel. Their niche overlaps in habitat use (rocky areas), reproductive seasons and food (arthropods).
- When Common spiny mouse was removed the Golden spiny mouse became nocturnal, suggesting temporal niche separation.

- **Morphological Niche separation- Character displacement**

The phenomenon by which character traits of two or more closely related species differ more when they occur together than when they occur in different geographical areas.



- **Conditional Niche separation – Thomas Park**

Worked on two species of flour beetles- *Tribolium confusum*, *Tribolium castaneum*

Competition between two species of flour beetles of the genus <i>Tribolium</i> at different temperatures and relative humidities					
Temperature	Humidity	EQUILIBRIUM POPULATION SIZE*		PERCENTAGE OF CONTESTS WON BY†	
		<i>T. confusum</i>	<i>T. castaneum</i>	<i>T. confusum</i>	<i>T. castaneum</i>
Cool	Dry	26.0	2.6	100	0
	Moist	28.2	45.2	71	29
Moderate	Dry	29.7	18.8	87	13
	Moist	32.9	50.1	14	86
Warm	Dry	23.7	9.6	90	10
	Moist	41.2	38.3	0	100

*Number of adults, larvae, and pupae per gram of flour.
†Based on 20–30 contests in each combination of temperature and humidity.
(Data from Park 1954, 1962.)

- Physical conditions can be critical for the outcome of competition
- Higher equilibrium size does not guarantee winning the competition. (2 – table)

Wildebeest (*Connochaetes taurinus*) Migration –

- in the Serengeti/Mara ecosystem of Tanzania and Kenya
- in the Serengeti migration, up to 1.4 million wildebeest plus, large numbers of zebra and Thomson's gazelles, move seasonally between dry and wet season ranges over a 30,000-km² area.
- Migration is ultimately driven by the marked and strongly seasonal rainfall gradient that runs from the south-eastern short-grass plains to the tall-grass woodland and savannah habitats in the north, centre, and west of the ecosystem.

This gradient imposes a constraint: at the end of the wet season, migrant species leave the plains as the latter dry up and green grass and surface water become confined to the wetter, northern reaches of the ecosystem. These constraints compel wildebeest and other migratory species to move north.



Wilde Beasts - Serengeti(Tanzania) Grasslands

Wildebeast migration 1) Adapted muscles- efficiency 56% 2) males create territories during mating period and defend them 3) birthing period (january), born calves can stand and run within a day and are able to keep pace with the migratory herd.

Why do 13-14 lakh Wilde beasts, a few lakh zebras, a few lakh gazelles, thousands of other assorted mammals migrate? (Year after year over a 30000 sq km area)

causes- food, water supply Sometimes they have to cross river while following the rain. Then they take the risk and cross the river even though some become prey of predators like crocodile

Not all Wilde Beasts migrate. Only the large herds do. Some groups stay.

Migration helps Wilde beasts in finding more food without being eaten.

Migration's impact on ecosystem Thousands drown in river crossings. (6500) = 10 blue whale carcasses Bones take 7 years to decay Increasing concentration of river

Become feast for many fishes (50% of diet of local fish is from the carcasses) The drowning is just 0.7% of the total herd.

It also Increases Tree cover (1980- present) Serengeti-Savanah

Leading to more diverse species. Increasing population of other animals too.

4 Competition

C4

Competition, Predation, Symbiosis

Population interaction

Succession - process of final biological system formation

each species has a unique niche in the community

Result of overlapping niche

hom. food,
temp.,
physiol. predation

No two species with the same niche can co-exist

(Darwin's principle)

Community
of
populations

competition

Not req. to have brutal force competition, can be show off etc.

Check: what's r , k and other parameters in models?

r → growth rate

N → no. of individuals in popn. Check!

K → carrying capacity

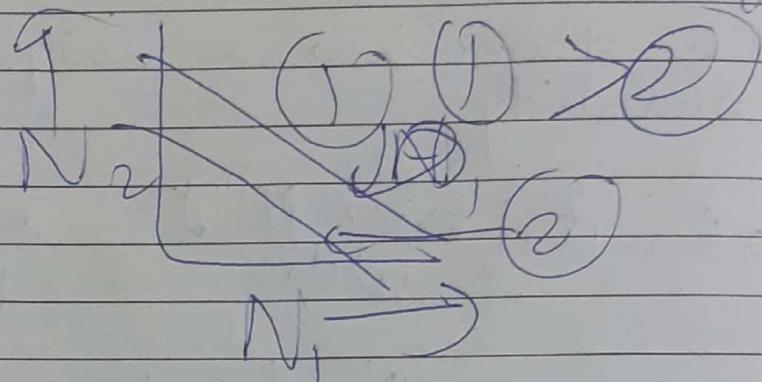
here, N , popn. will increase

here N , popn. will decrease

N_1

In reality, K & R are ~~independents~~,
but in model, they are ~~constant~~
PAGE NO.

Populus - simulation website
or software



$x_1, x_2 \rightarrow$ density dependent,
hence not necessary

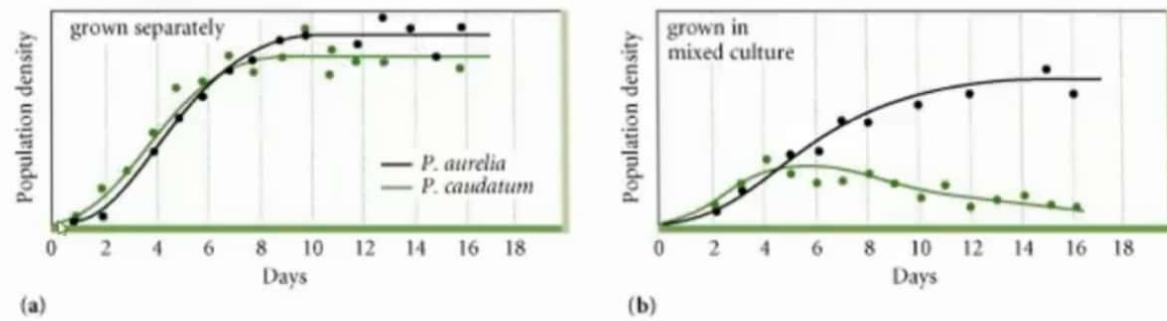
Organism's popn. that straight
balanced at certain lines are disturbed
place can go unbalanced in N_1 vs N_2
(both ↑ at other place) graph

non-native organisms will disrupt
ecosystem

Are we humans the invasive
species?

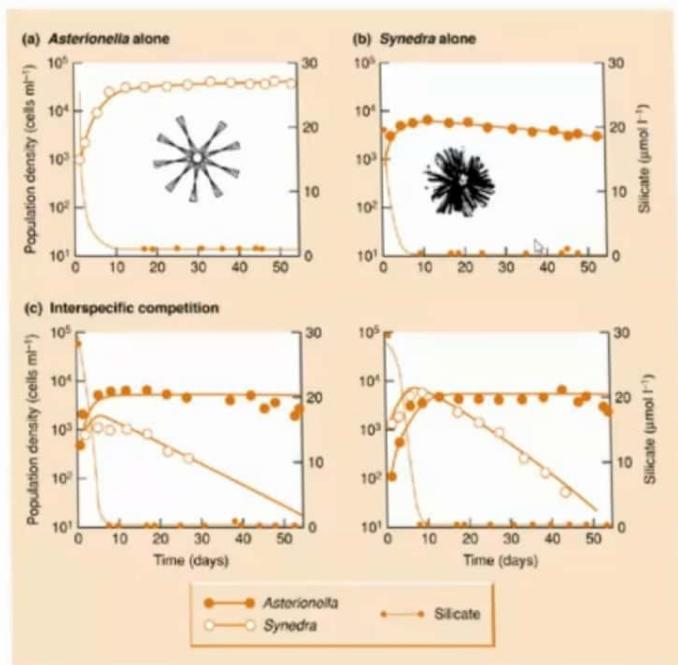
→ What to do? instead of killing, use
them

Early experiments: Gause's principle of competitive exclusion



No two species with the same niche can co-exist.

Later experiments: Tilman et al (1981)



Two species can not coexist on a single limiting resource



What is competition?

"Any use or defense of a resource by one individual that reduces the availability of that resource to other individuals."

Two groups use the same limited resource, or seek that resource, to the detriment of one or both.

Two types based on the kind of competitors

Intraspecific (Between members of the same species)

Interspecific (Between members of different species)

Intra-specific competition

One example: Density-dependent reduction in population growth rate (already discussed)

Another major example: Competition for mates (more details when we discuss sexual selection)



Video 2

https://www.youtube.com/watch?v=hx-Q1k_9SwA

Interspecific competition

Two populations of different species competing with each other for the same limiting resource. If the species do not affect each other, then there is no competition.

Features of interspecific competition:

- nontrophic interaction (one species does not eat the other)
- reduced population growth rate or equilibrium number for both or at least one of the populations



1, 2

$$\frac{dN_1}{dt} = \alpha_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = \alpha_2 N_2 \left(\frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right)$$

Lotka-Volterra competition eqn.

Inter-specific
comp. co-eff.

$$\frac{dN_1}{dt} = \alpha_1 N_1 \left(\frac{K_1 - N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1} \right)$$

$$\frac{dN_1}{dt} = \alpha_{12} N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right)$$

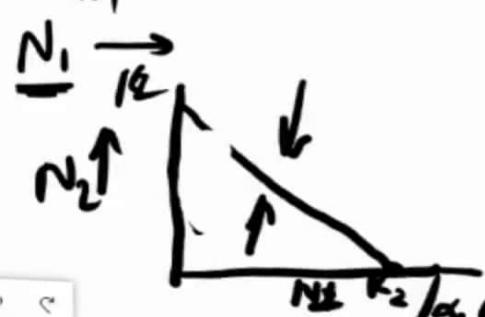
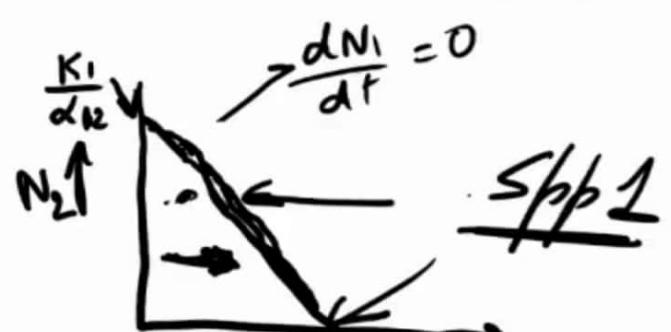
When $\frac{dN_1}{dt} = 0$

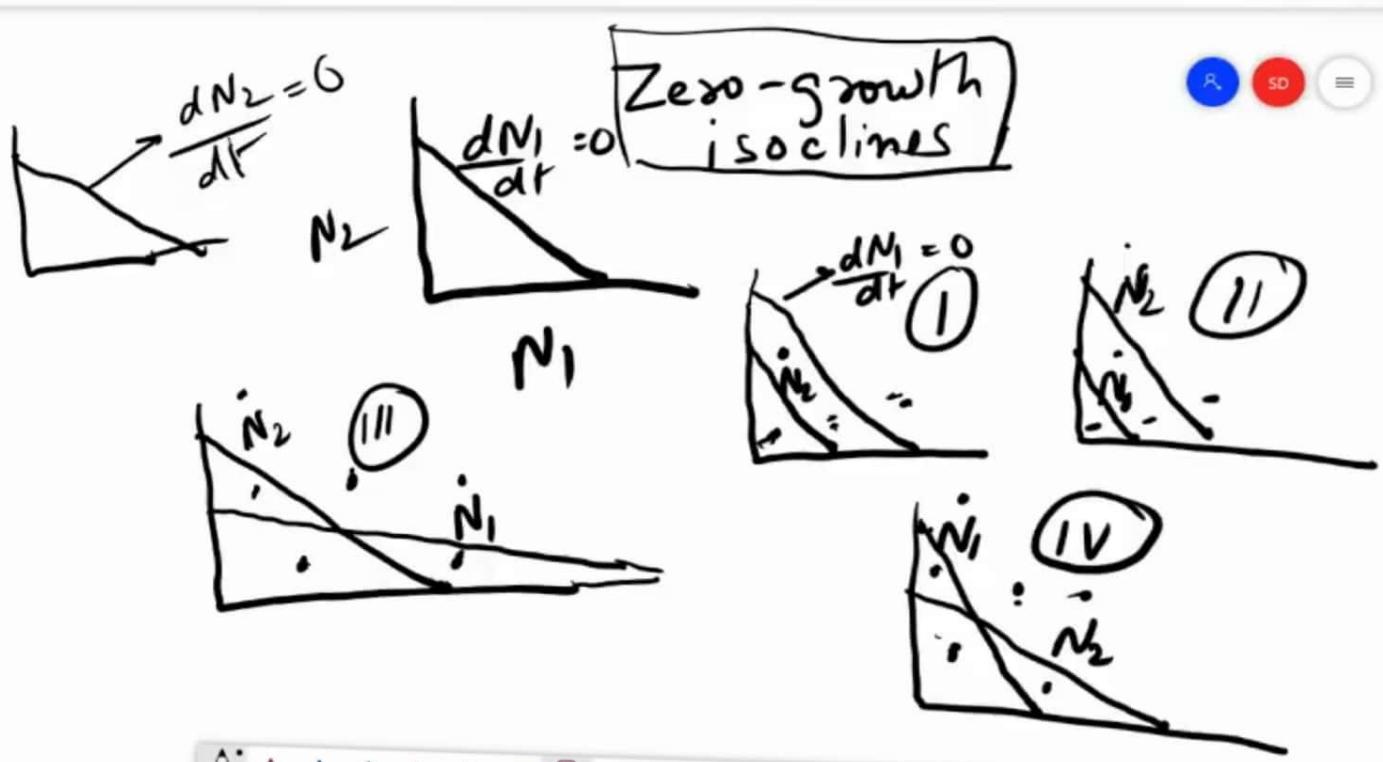
$$K_1 - N_1 - \alpha_{12} N_2 = 0$$

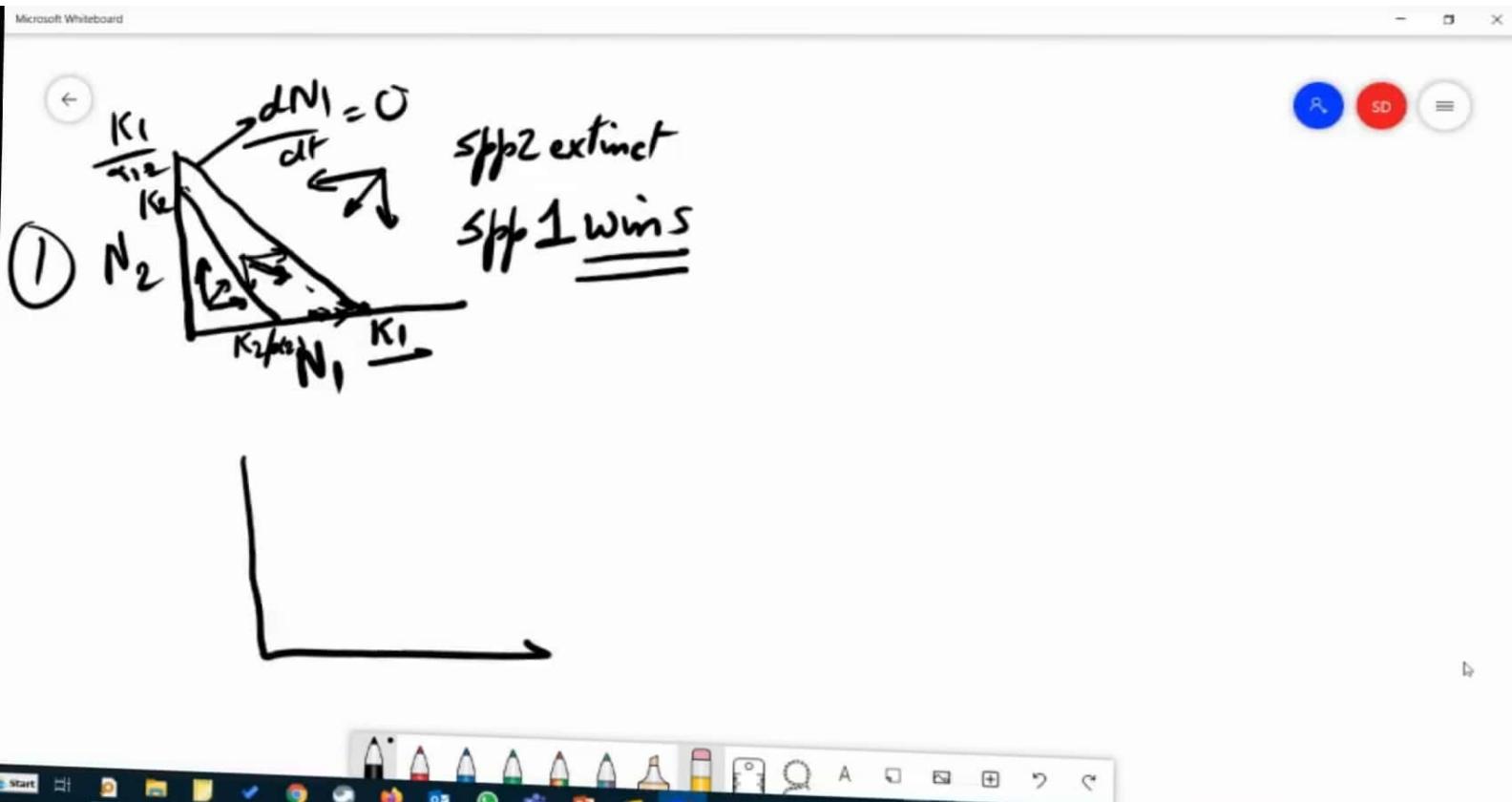
$$\Rightarrow N_2 = \frac{K_1}{\alpha_{12}} - \frac{1}{\alpha_{12}} N_1$$

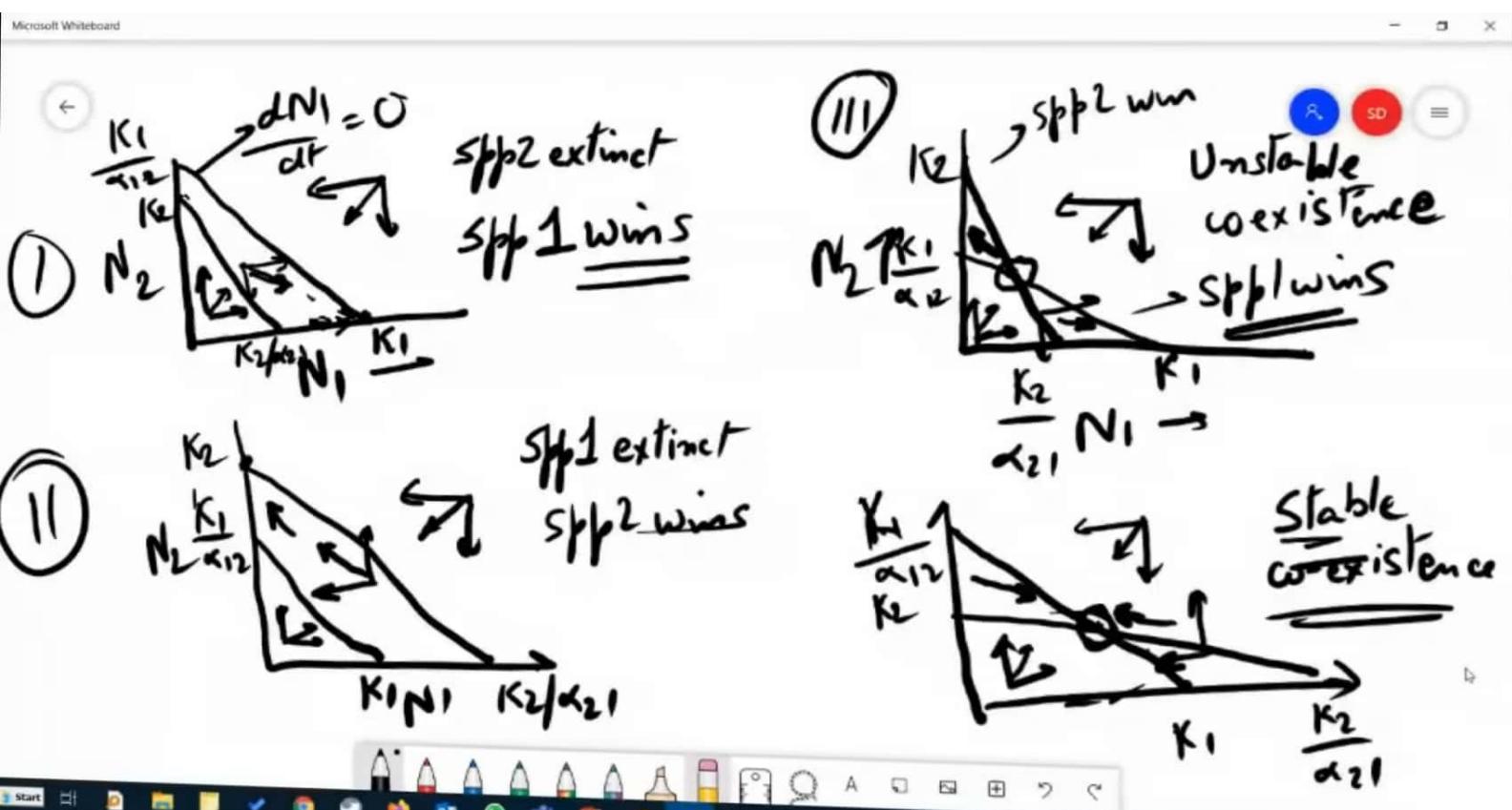
$$- K_1 - (N_1 + \alpha_{12} N_2)$$

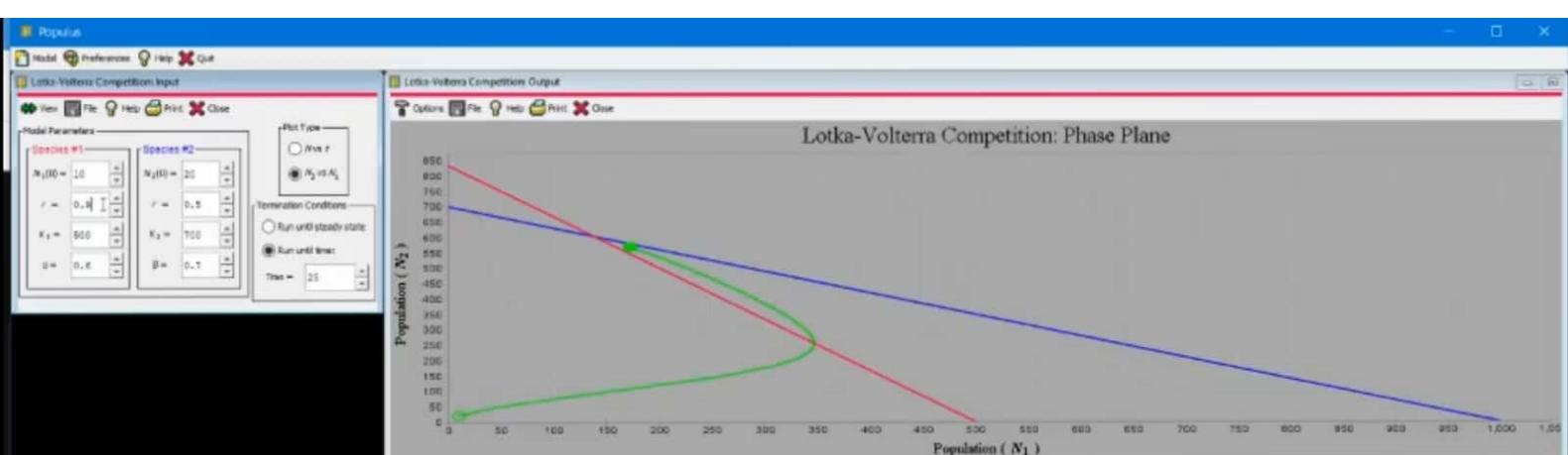
$$N_1 = \frac{K_2}{\alpha_{21}} - \frac{1}{\alpha_{21}} N_2$$

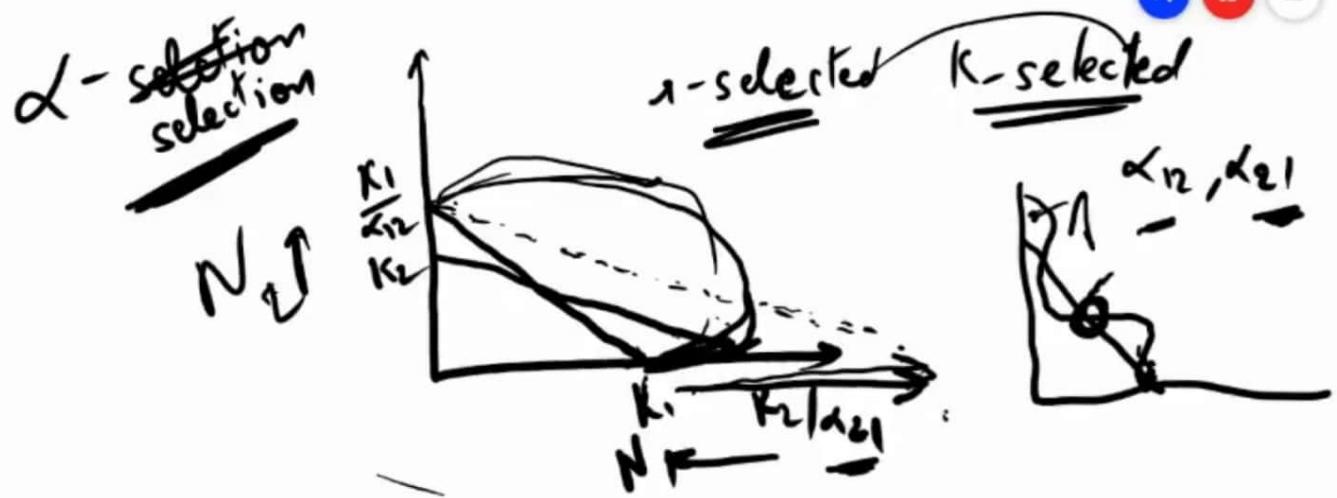












Clear canvas

Closer home: Effects of the 2018 and 2019 floods in Kerala



a



b

a. *Arapaima* after the 2018 floods. Can grow upto 200 kgs

b. Alligator gar caught from the Kurumali River. Can grow upto 137 kgs

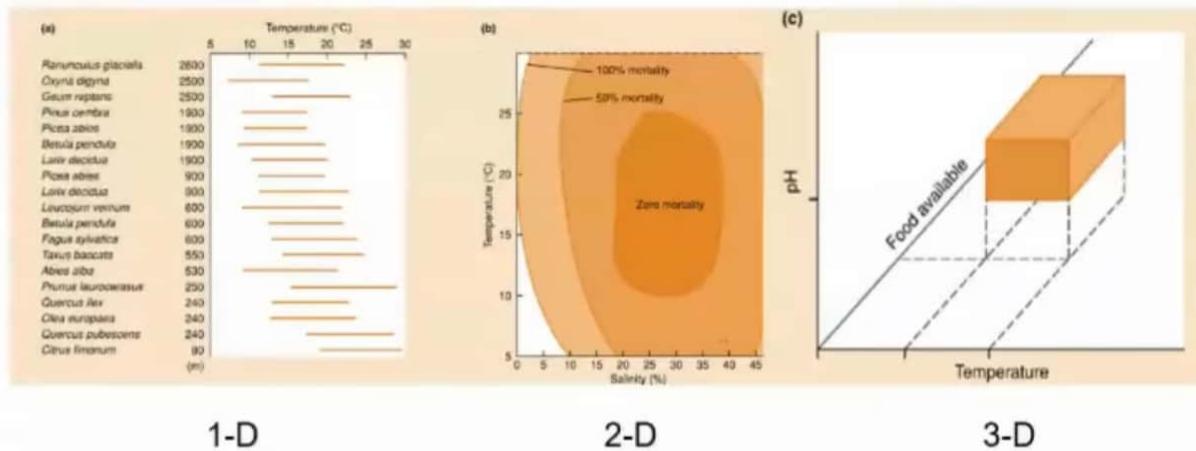
Case of the competition avoiders

The glaring examples of invasive species notwithstanding, in nature, lots of species with similar niches do seem to co-exist.
How is that possible?

Before that, what is a niche?



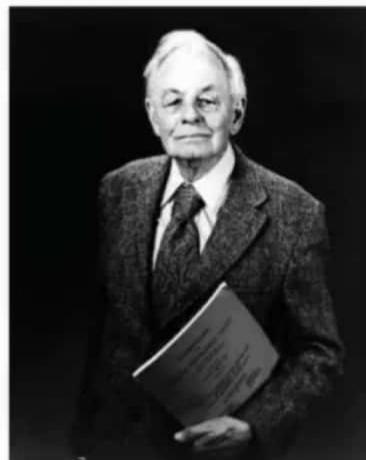
Ecological Niche: n-dimensional hypervolume



- (a) A niche in one dimension. The range of temperatures at which a variety of plant species from the European Alps can achieve net photosynthesis of low intensities of radiation (70Wm^{-2}).
- (b) A niche in two dimensions for the sand shrimp (*Crangon septemspinosa*) showing the fate of egg-bearing females in aerated water at a range of temperatures and salinities.
- (c) A diagrammatic niche in three dimensions for an aquatic organism showing a volume defined by the temperature, pH and availability of food.

Population-Persistence Niche

“ecological niche” is “a quantitative description of the range of environmental conditions that allow a population to persist* in some location”.



GE Hutchinson



*persist = positive growth rate

From Ecological Niche by TW Schoener

Resource-Utilization Niche

“focuses entirely on what members of a species population in some locality actually do—in particular, how they use resources.”



Robert McArthur



Richard Levins

From Ecological Niche by TW Schoener



Resource-Utilization Niche

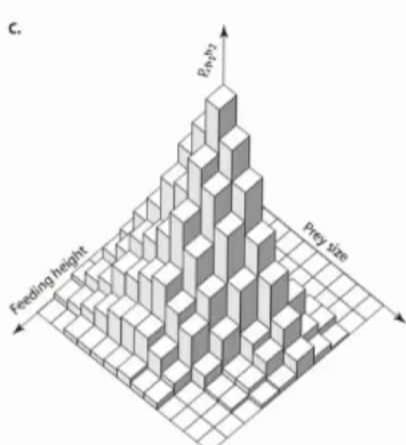


Figure 3. An example of the resource utilization niche. [A] A one dimensional niche, where the dimension is prey size. Numbers give prey size categories, indexed by h ; [B] the same utilization smoothed; [C] utilization of two resource dimensions, prey size and feeding height. (Redrawn from Schoener, 1986.)

Kinds of niche axes typically used for utilizations
Habitat

microhabitat (e.g., height in vegetation)

macrohabitat (e.g., vegetation zone such as tropical rainforest or desert)

Food type

food size
hardness

Time

daily activity

seasonal activity

From Ecological Niche by TW Schoener

Niche Theory: Present Status

Ecology's love-hate relationship with the niche concept has been long and not especially pretty.

—N. G. Hairston Jr. (1995)



So when is co-existence possible?

**If there is a separation / partitioning
of the niche**

Resource partitioning:

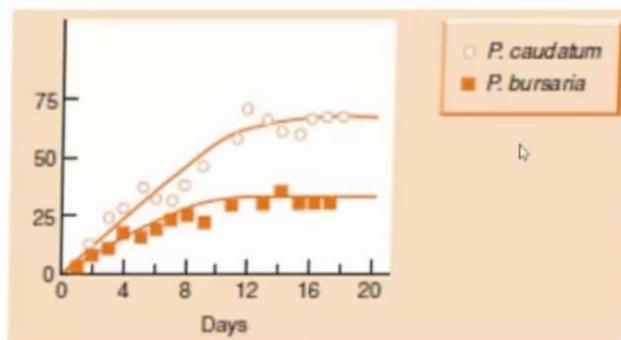
- Spatial
- Temporal
- Morphological

Conditional niche differentiation



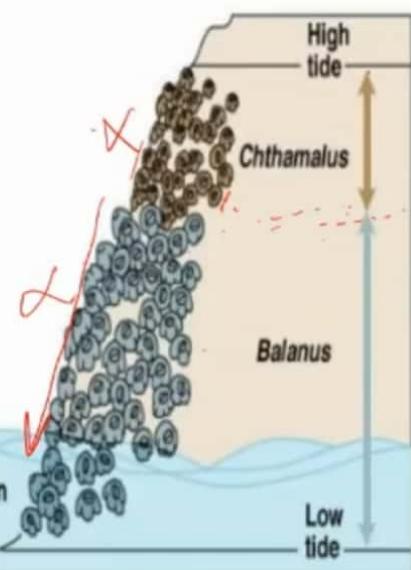
Spatial niche separation #1

Gause's experiment on *Paramecium caudatum* and *P. bursaria*

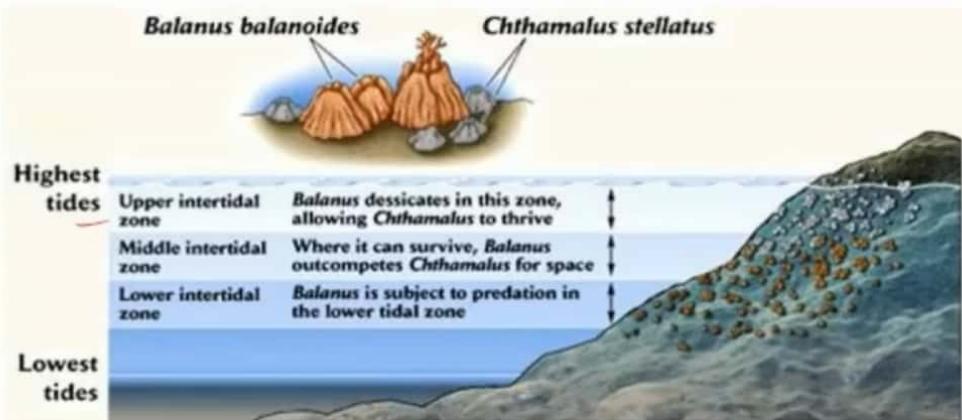


***P. caudatum* and *P. bursaria* coexist as the former feeds on the top layers of the culture while the latter feeds on the bottom layers.**

Spatial Niche separation #2, Connell's barnacles



What is happening:



Question:
Why such a distribution?

Temporal niche separation



Common spiny mouse
(*Acomys cahirinus*)
Nocturnal



Golden spiny mouse
(*Acomys russatus*)
Diurnal

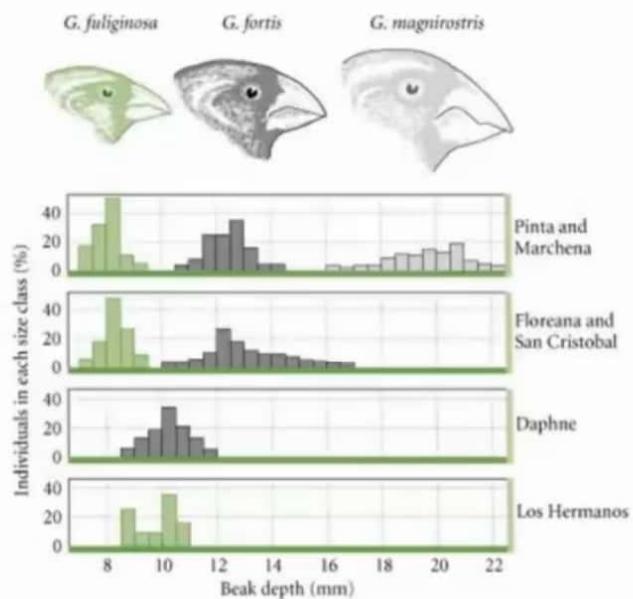
- Co-exist in the deserts of Israel
- Overlap in
 - habitat use (rocky areas)
 - food items (prefer arthropods)
 - reproductive seasons

When the common spiny mouse were experimentally removed, the golden spiny mouse became nocturnal, suggesting temporal niche separation!

(Shkolnik, 1971, Kronfeld-Schor & Dayan, 1999)



Morphological niche separation: Character displacement



The phenomenon by which character traits of two or more closely related species differ more when they occur together than when they occur in different geographical areas.

Conditional Niche separation: Thomas Park (1954, 1962)

Worked on two species of flour beetles

Tribolium confusum

Tribolium castaneum

TABLE 21-1 Competition between two species of flour beetles of the genus *Tribolium* at different temperatures and relative humidities

Temperature	Humidity	EQUILIBRIUM POPULATION SIZE*		PERCENTAGE OF CONTESTS WON BY†	
		<i>T. confusum</i>	<i>T. castaneum</i>	<i>T. confusum</i>	<i>T. castaneum</i>
Cool (24°C)	Dry (30% RH)	26.0	2.6	100	0
	Moist (70% RH)	28.2	45.2	71	29
Moderate	Dry	29.7	18.8	87	13
	Moist	32.9	50.1	14	86
Warm (34°C)	Dry	23.7	9.6	90	10
	Moist	41.2	38.3	0	100

*Number of adults, larvae, and pupae per gram of flour.

†Based on 20–30 contests in each combination of temperature and humidity.
(Data from Park 1954, 1962.)

Physical conditions can be critical for the outcome of competition

Higher equilibrium size does not guarantee winning the competition

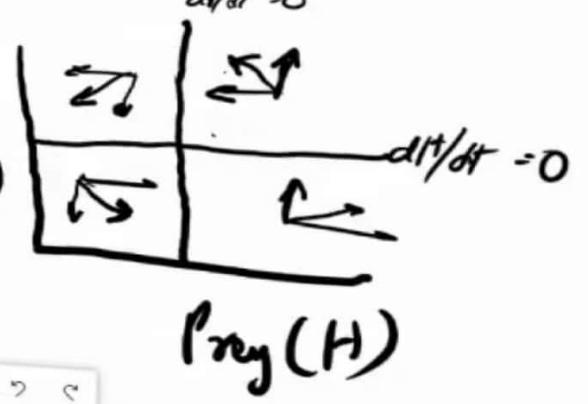
\leftarrow st $H \xrightarrow{t} H$
 Predator $\rightarrow P$

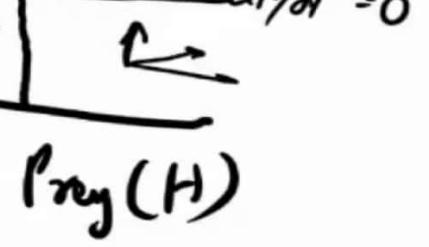
$\frac{dH}{dt} = \alpha H - \underline{\alpha HP} \rightarrow \underline{\text{Prey eqn}}$

$\frac{dP}{dt} = \underline{c\alpha HP} - \underline{mP} \rightarrow \underline{\text{Predator eqn}}$

$\frac{dH}{dt} = 0$
 $\alpha H = \alpha HP$
 $\Rightarrow P = \frac{H}{\alpha}$
 $c\alpha HP = mP$
 $H = \frac{m}{c\alpha}$



$\frac{dP}{dt} = 0$
 $\underline{dP/dt = 0}$


 $\frac{dH}{dt} = 0$
 $\underline{dH/dt = 0}$


Make the prey growth density dependent

$$dH/dt = rH(1-H/K) - pHP$$

$$dP/dt = aPH - mP$$

Solve it now and tell me what it shows...

Populus simulation

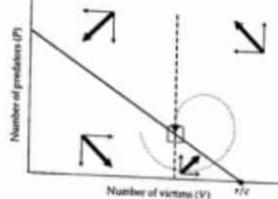


Figure 6.5 The effect of a victim carrying capacity on the victim isocline. The victim isocline slopes downward with a carrying capacity incorporated. The intersection with the vertical predator isocline forms a stable equilibrium point.

Click to add notes

5 Predation

CHAPTER 5 :-

Part 1 → Predation :-

Predation → process → 1 organism eats part/full → another organism

Herbivory → Animal eats plants

Carnivory → Animal or plant eat ~~or other~~ other animal(s)

Parasitism → laying eggs on or near host killed by offspring

Parasitism → live on or in host, don't kill

Cannibalism - - - -

Predator and prey number vary in sync with each other.
But is it intrinsic or extrinsic factors causing this?

Prey is called Host → $H \rightarrow$ no. of H

Predator " Predator → $P \rightarrow$ no. of P

$$\text{Prey eqn} : - \frac{dH}{dt} = rH - aHP$$

↓ constant

$$\text{Predator eqn} : - \frac{dP}{dt} = c(aHP) - mP \rightarrow \text{death}$$

↓ another constant

↓ death rate

$$\text{if } \frac{dH}{dt} = 0$$

$$\therefore rH = aHP$$

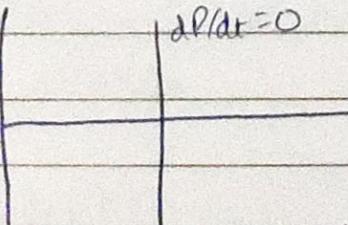
$$P = (r/a) \rightarrow \text{constant}$$

$$\text{if } \frac{dP}{dt} = 0$$

$$caHP = mP$$

$$\therefore H = m/ca \text{ (constant)}$$

Pred (P)



Prey (H)

$$\frac{dP}{dt} = 0$$

$$\frac{dH}{dt} = 0$$

Watch from 20:00 for Populus graph.

the Lotka Volterra model:-

assumptions:-

→ Growth of victim population is limited only by predation and nothing else else.

→ Prey Predator only survives if victim is present

→ No change in environment

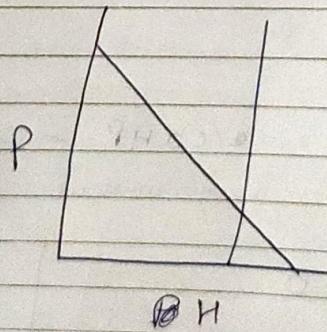
→ Predator and prey encounter each other randomly.

Part -2 -

① Do we make the prey eqn density dependant:

$$\frac{dH}{dt} = rH \left(1 - \frac{H}{K}\right) - pHP$$

$$\frac{dP}{dt} = \alpha pHP - mP$$



Rosenzweig MacArthur Model:

R.M makes assumption that isolines are straight lines
and explicitly builds in density dependence

Net logo Wolf Sheep Model (700)

- 1st Model → Wolf + Sheep
- 2nd Model → wolf + sheep + grass

1st model :-

whenever W and S interact, possibility of kills.

Grass assumed infinite

(like Luca Volterra)

~~reproduction~~ Simulation starts at 11:33

~~first encounter~~

Each simulation gives different result even with same conditions.

Gause's expt. on Paramecium (P) and Didinium (D)

a) No refugia :- extinction

Refugia → a safe space
for P away from D

b) Refugia :- "

c) Constant immigration of P and D :- Adding 1 P and

1 D every 3 days led to sustained oscillations

Conclusion :-

System if left to itself will ~~be~~ lead to extinction. Constant interference from outside.

Still not perfect

Grause's experiments relied on homogeneity of the environment

Huffaker's Experiment:

Used two types of mites on spatially distributed oranges.

Took orange, put wax paper on majority of orange.

1 orange put prey and predator, both extinct
2 oranges, connected them with silk thread, both extinct.

Then made more complex.

Got sustained oscillations when using 48 spheres (some oranges, rest plastic balls).

- Distribution and relative abundance of mites changed over time
- Preys need some advantage to survive
- Metapopulation promote prey survivorship through extinction - relocation
- if predator is efficient prey can survive only in patches

Predators can save & can reduce prey populations better than pesticide.

Different types of dynamics are observed because -

- multi prey multi predator
- spatial heterogeneity
- Predator efficiency
- Evolutionary changes

Predation is a strong pressure that forces evolution to avoid predation.

Biggest change → Speed, Armor or spikes, camouflage

Chemical Warfare → poison dart frog, ~~the~~ Skunks

↳ those who use this usually are distinctly coloured warning colours

Batesian Mimicry:-

Harmless animal mimics a dangerous animal to scare predators

Mullerian Mimicry :-

Two dangerous or unpalatable species resembling each other:-

► Monarch Butterfly and Viceroy Butterfly

This is called co-evolution.

Predators adapt to kill prey, prey adapt to escape predation.

~~Chapter~~ Part 3 :-

strategies for predation predator avoidance:- coloration

Aposematic coloration :-

warning colors that make a dangerous, poisonous, or foul tasting animal recognizable by a predator

There is camouflage

The third way is mimicry:-

Major types:-

Batesian and Mullerian

Behavioral :-

1. Catalepsis :-

Prey playing dead

2. Intimidation display:-

Attempting to startle the predator

3. Group living.

Chemical :-

Poison, smell

6 Eutrophication

Chapter 6 :-

Part 1 :-

Story of Retreat of Aral Sea :-

Water from rivers feeding the sea was used for irrigation, without regards for consequences, leading to the lake getting divided into 2.

Now, with dam, water levels are rising.

Aral Sea was 4th largest in world in 1960

1962 → Soviet govt. diverted water for cotton irrigation

With help of World Bank, situation improved until ~~2018~~ April 2018, regression.

Shrinking of sea led to increase in salinity.

Use of weapons and fertilizers caused problems.

Fisheries collapsed.

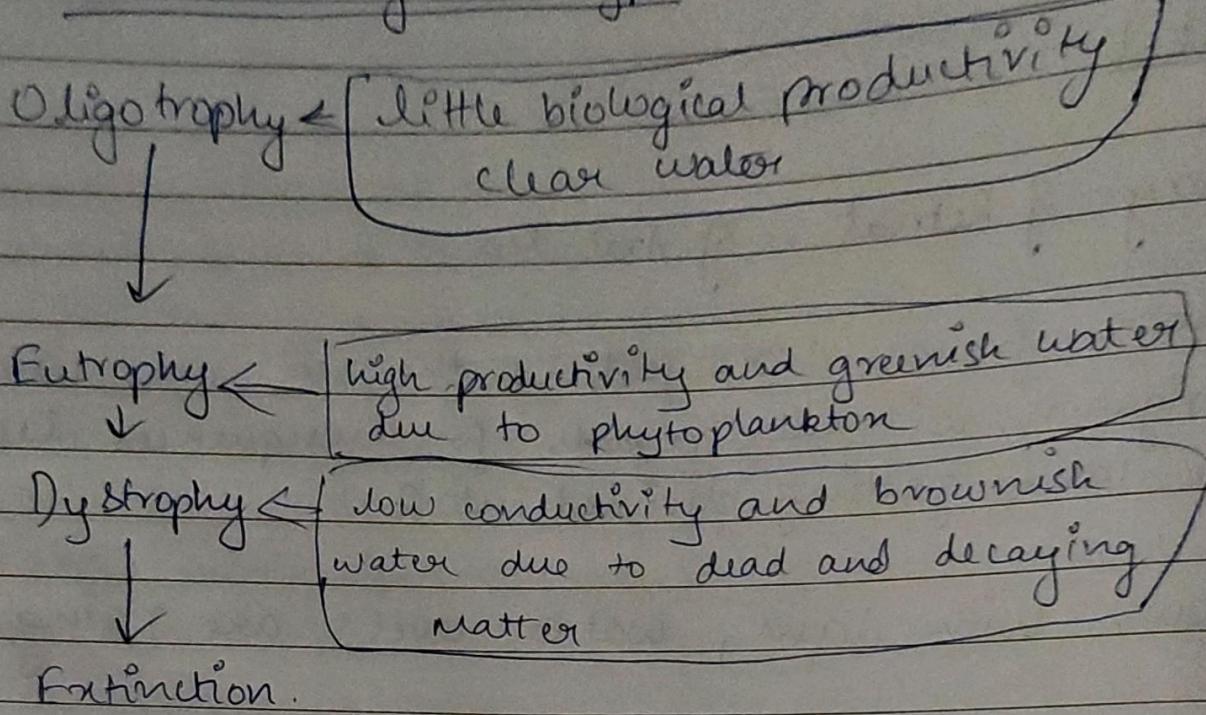
Fish sp. → 32 to 6

Bird sp. → 319 to 160

Mammals → 70 to 32

However, even without human intervention, most lakes suffer same fate due to a phenomenon called eutrophication.

Classical view of Lake Types :-



This is not fixed. Some lakes remain fixed in one particular stage.

Modern View of Lake Types :-

Oligotrophic and eutrophic can be separated by established limits (P_{tot} concentration during spring circulation)

Phosphate

- Ultradoligotrophic : $P_{tot} < 5 \mu\text{g l}^{-1}$
- Oligotrophic = $5 - 10 \mu\text{g l}^{-1}$
- mesotrophic → $10 - 30$
- eutrophic → $30 - 100$
- hyper-eutrophic → > 100

This is just one aspect.

Factors determining trophic levels:

1. Depth

2. Nature of drainage basin:-
erosion rate, soil composition

3. Climate

4. Human activity (cultural eutrophication)
→ Fertilizers
→ Human waste (Domestic, Industrial)

How does trophic condition change?

1. Nutrient enrichment

→ Natural

→ Human intervention

2. Increased organic production (Algal Bloom)

→ Blue green algae (Anabaena, Mycocystis)

→ More algae → more oxygen consumption

→ less sunlight

→ anaerobic reactions ↑

→ pH ↑

3. Deaths of fishes and aquatic life forms.

This doesn't occur only in small lakes.

PART 2

How to reverse Eutrophication

Story of Lake Washington:-

1940s → oligotrophic

1950s - 1960s → Sewage into lake

stink became so much, call lake Stinko.

→ Sewage was implicated *in 1970, sewage diverted to sea.

With reduction in P-level, lake condition improved.

Detergent manufacturers reduced P-levels.

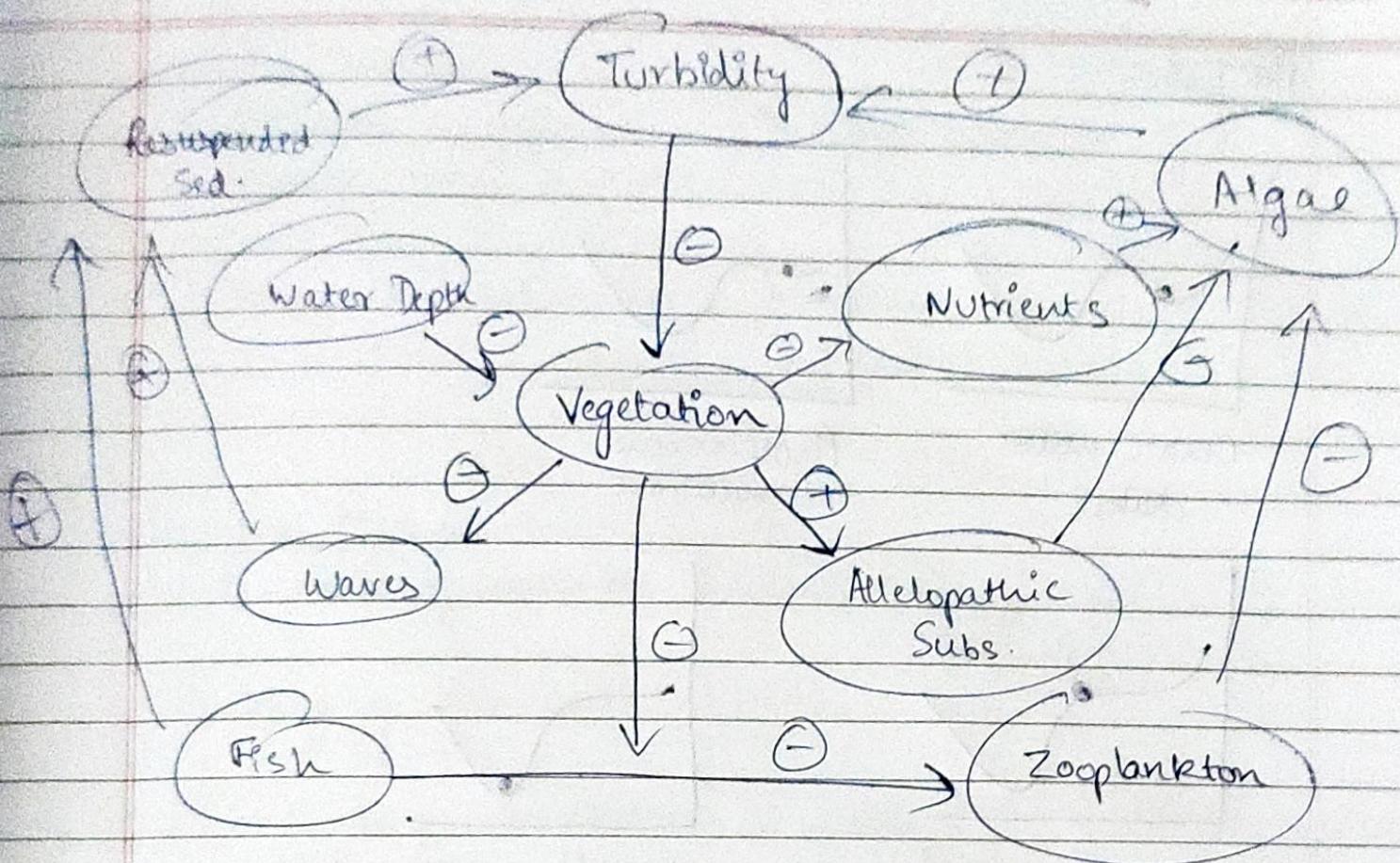
Daphnia → filter feeder ~~crustaceans~~ crustaceans, their return improved lake condition.

Phosphate levels when mapped against charophyte vegetation shows hysteresis. Just by reducing phosphate levels we cannot restore lost vegetation.

Need to reduce phosphate levels by a huge amount for results.

INTERACTION IN SHALLOW LAKES

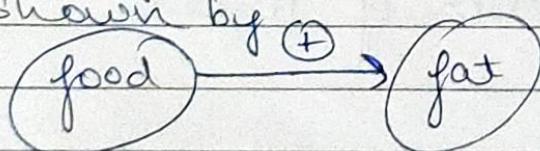
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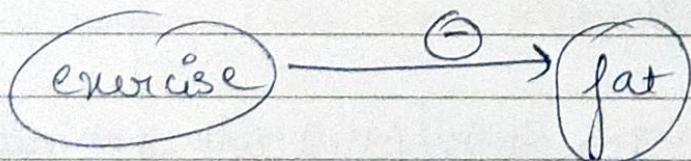
increase in

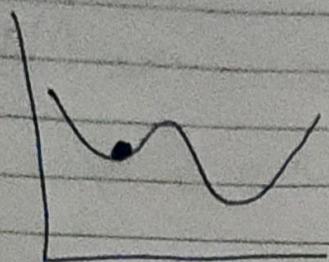
The sign shows effect the arrow tail will have on arrow head.

for example, if there is more food, we will get fat
this is shown by

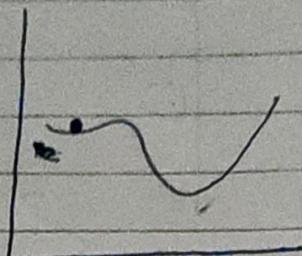


if we exercise more, we will have less fat

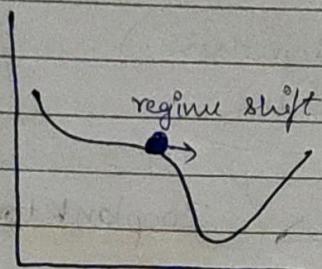
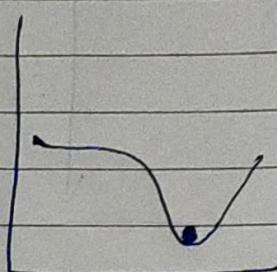


PART 3:-

clear water lake



Phosphorous accumulation

flooding, warming
warming

turbid water lakes

How to reduce trophic states?

Reduce the number of fishes.

Physical methods:-

1. Sediment dredging (P rich sediment is removed)
→ is costly
 2. Dilution / flushing → it is filled with nutrient poor H₂O.
 3. Increasing water level, reduces risk of resuspension
- Bottom ←
of lake
- Hypolimnetic withdrawal :- Using pipes, remove water from bottom part.

Chemical Methods:-

1. Hypolimnetic Oxygenation:- increases sorption of P.
However takes > 10 yrs.
2. Phosphorus inactivation:- aluminum salts or P-binding agents used.

Biological Methods:-

- Removal of ~~zooplankton~~ zooplankton fishes
- Stocking of fish eating fish
- Introducing mussels to ~~increase~~ increase water filtration.

7 Conservation Biology

Chapter 7

Part 1:-

Conservation Biology

Art of making sure non human species don't go extinct.

Humans are directly linked to increased extinction rates.

John Muir

Romantic Transcendental Preservation ethic

Assumed "communication with nature" bring people close to God.

Conclusion:- Preserve

Gifford Pinchot :-

First chief :- US Forest Service

Protégé of Dietrich Brandis

(First Inspector general of forests in India)

Conservation = "art of producing from forestry for service of man whatever it can yield."

Conclusion - Economic ~~management~~

Management

Aldo Leopold :-

American Naturalist :-

"A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community. It is wrong when it tends otherwise."

Conclusion - Conservative

what determines Vulnerability of species

Rabinowitz's rarity classification

Range of distribution

Tolerance	Broad	Extensive		Restricted	
		Large pop. size	Small pop. size	Large pop. size	Small pop. size
	Narrow	Large Small		Large Small	

Why are small populations likely to be more vulnerable?

Ans:-

1. Demographic Stochasticity :- Random variation in birth, death rates, sex ratio etc.
2. Genetic stochasticity :- Genetic drift leading to inbreeding depression (recessive traits get selected more).
3. Environmental stochasticity and natural catastrophes.

for conservation:

Science, common sense, economics and politics must work together.

Part 2:- Project Tiger

Estimated tigers in 1900 \rightarrow 40-45 thousand

Number of tigers in 1972 \rightarrow 1827

Reasons:-

Hunting, habitat destruction, loss of prey, poaching
by villagers

Project Tiger launched on 1st April 1973

Aim:-

ensure maintenance of viable population for scientific, economic, aesthetic, cultural and ecological values.

What was done:-

Criteria for selecting areas:-

- experienced little disturbance
- high development potential for both predator and prey
- no mining, drilling, mining etc.
- were in different states.

first 9 tiger reserves total area $\rightarrow 13017 \text{ km}^2$

Bandipur, Corbett, Kanha, Manas, Melghat, Palamau, Ranthambore, Simlipal, Sunderbans.

Activities:-

- establish buffer area
- connect habitats through corridors
- halting cattle activities
- regular patrolling

Numbers went up initially

Problems:-

- farmers angry
- encroachments
- Poaching
- reduction in prey
- lack of funds

2018 \rightarrow 2461 tiger photos captured.

8 Evolution

Chapter 8:-

Part 1:-

Evolution:-

Observation of nature (living organisms), the diversity and pattern of diversity is not random.

Can make a hierarchy (Biological trees).

Earliest theories → Plato and Aristotle

(Theorised that all organisms were created as we see them)

Lamarck:-

Bigest thought → Inheritance of Acquired characters

Just took the most popular theory and wrote it in his ~~own~~ words

Charles Darwin :-

Natural Selection.

Darwin's theories:-

- Every species is composed of numerous local populations.
- Every individual is unique

Darwin's arguments :-

1. More offsprings are produced than environment can handle.
2. individuals vary
3. Competition for resources due to variation
4. individuals with favourable variations leave more offsprings.
5. Variations can be inherited.

→ differences in reproductive output leads to subtle changes in traits, accumulation of this over long periods leads to new species.

Darwin put lot of emphasis on competition

Consequences of Darwin's train of thought :-

- Non constancy of species
- Descent of organisms from common ancestor
- Gradualness of evolution
- Multiplication of species
- Natural selection is a mechanism
- Historic nature of evolution

Opposition to Darwin:-

- He didn't give mechanism of inheritance

Part 2:-

Biometriicians vs Mendel:-

Mendel proposed traits to be discrete, but most traits studied were continuous.*

Mendelian mode of inheritance couldn't account for continuous traits evolution of continuous traits

→ Conclusion:-

Discrete traits inherited by Mendelian genetics
Continuous traits follow different inheritance mechanism.

* discrete → tall or short, fat or thin

continuous → whole range of height or weight etc.

~~scribble~~ :-

However, Bateson and DeVries found out that degree of variation found in continuous traits is ~~too~~ insignificant.

The resolution was :- (R.A. Fisher)

Continuous traits can be thought of as combined action of multiple genes.

Modern Synthesis (1950s) :-

The major tenets of evolutionary synthesis:-

→ populations have genetic variation caused due to random mutation and recombination (true, but other sources of variation exist)

→ populations evolve by changes in gene frequency brought about by random genetic drift, gene flow, and natural selection.

→ ~~most~~ most adaptive genetic variants have individually slight phenotypic effects, so that phenotypic changes are gradual.

→ Diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations.

Extended Evolutionary Synthesis :-

1. There has been no major paradigm shift.

Part - 3 :-

Epigenome → tightly wraps the inactive genes, while it lets active part get easily read.

Epigenome is the complete description of all the chemical modifications to DNA and histone proteins that regulate gene expression.

Rat mothers → lick and groom offspring a lot → offspring ^{becomes} relaxed adult
↳ " " " " little → " " anxious "

Thus, behaviour not completely genetic dependant

Nurturing reduces methylation of promoter, increasing the expression of GTR gene and hence offspring is more relaxed as an adult.

Thus, environment can also sometimes alter the genome.

Some acquired traits can be inherited (epigenetics)

Genetic information can be passed across species.

9 Selection

Chapter 9 - Selection :-

Natural selection is the differential survival and reproduction of individuals due to differences in phenotype.

Best study of natural selection is the Galapagos finches

- If there is variation within breeding groups
- If part of the observed variation is inheritable
- If some individuals are more successful in reproduction than others
- If variation influences fitness
- **THEN** → those with most favourable phenotype is selected naturally

(Galapagos) is a "natural laboratory" :-

- replica populations relatively isolated on different islands (almost essentially practically 1 species of finches on each island)
- small islands so census is easy
- Survival, reproductive success and morphology can be studied onsite

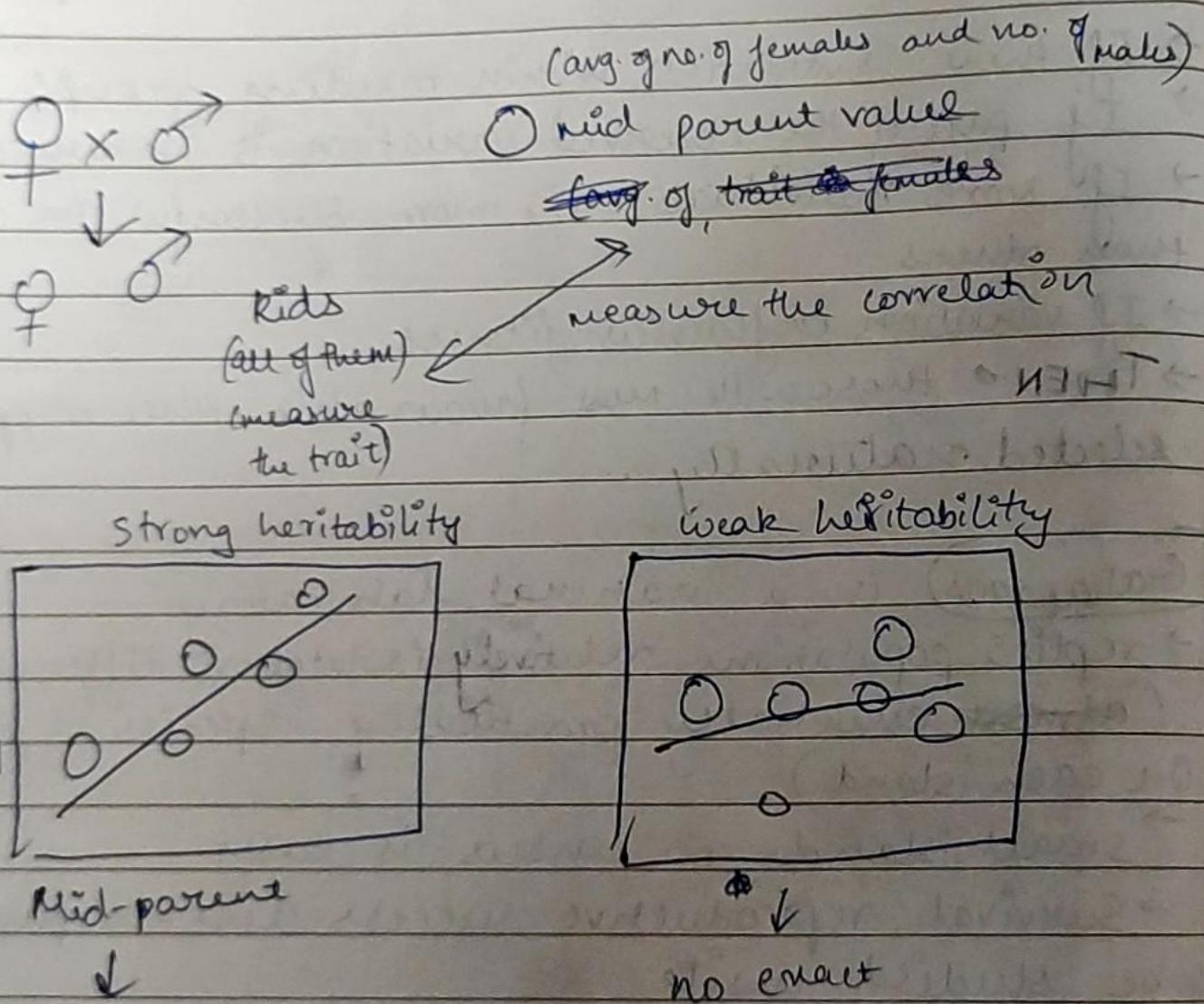
→ 45 islands, owned by Ecuador, volcanic in origin

Darwin's finches → 14 species born from a single flock that migrated there 2-3 million years ago. (main difference is in beak shape and size, due to different food available.)

To test inheritance capabilities:- check for similarity between few relatives, parents and offsprings.

Genetic variation is observed in finches in their beaks. Different species have different beak sizes to help in foraging.

Selection only changes population if change is heritable.



if heritability $> 0.2 \rightarrow$ greater response better to selection

human height heritability ≈ 0.6

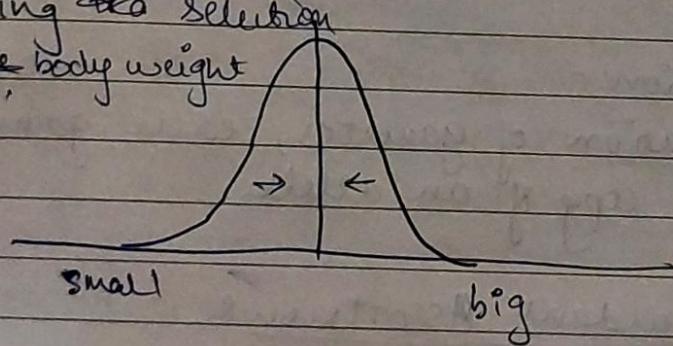
Bigger beaks aren't always better :-

- poorer at manipulating smaller objects
 - more energetically expensive to produce
 - Affects vocal communication, other aspects of mate choice
- ⇒

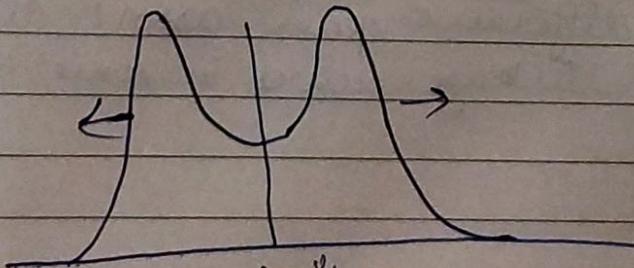
Major lessons:-

1. Evolution can occur very rapidly and dramatically (during sudden drastic environmental changes)
2. Source of natural selection shift, direction of evolution changes
3. This ~~saw~~-saw change gives an impression that evolution is gradual

Stabilizing ~~&~~ selection
~~body size, body weight~~



Disruptive :-



example → large and small beaked finches

Natural selection acts on phenotypes, but change only occurs when allelic frequencies change

Individuals vary in survival and reproduction. When genes they carry contribute to differences in fitness, evolution occurs.

→ Natural selection changes gene frequencies in populations AFTER exposure to selection

CHAPTER - 10 PART - 1 :-

Population genetics

Mendel's laws:-

Law of segregation:-

During formation of gametes, each gamete gets just one copy of an allele

Law of Independent Assortment :-

Alleles of different genes assort differently (However, linkage occurs in some trait).

10 HW Law

Natural selection acts on phenotypes, but change only occurs when allelic frequencies change

Individuals vary in survival and reproduction. When genes they carry contribute to differences in fitness, evolution occurs.

→ Natural selection changes gene frequencies in populations AFTER exposure to selection

CHAPTER -10 PART -1 :-

Population genetics

Mendel's laws:-

Law of segregation:-

During formation of gametes, each gamete gets just one copy of an allele

Law of Independent Assortment :-

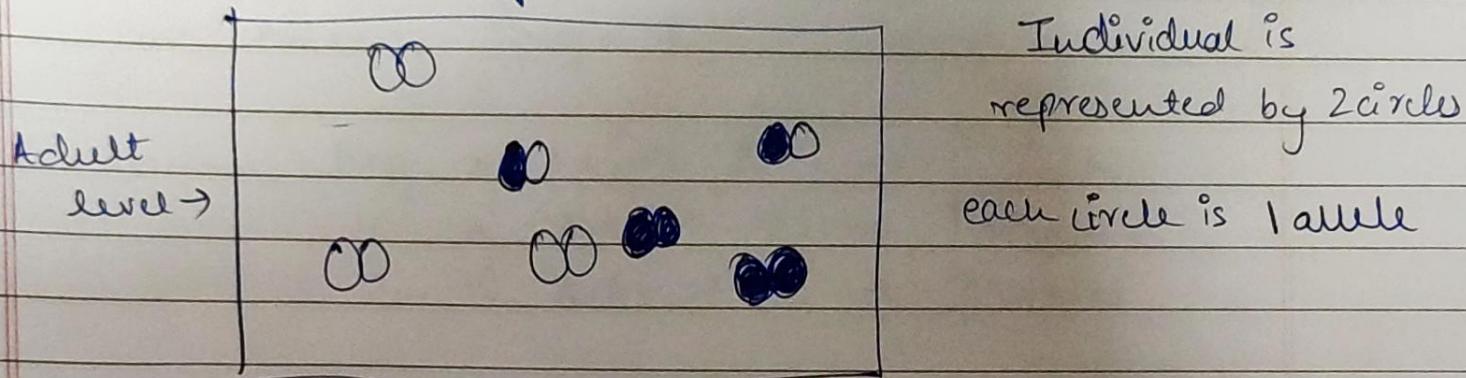
Alleles of different genes assort differently (However, linkage occurs in some trait).

Population genetics explains change in gene frequency in a population over a time t .

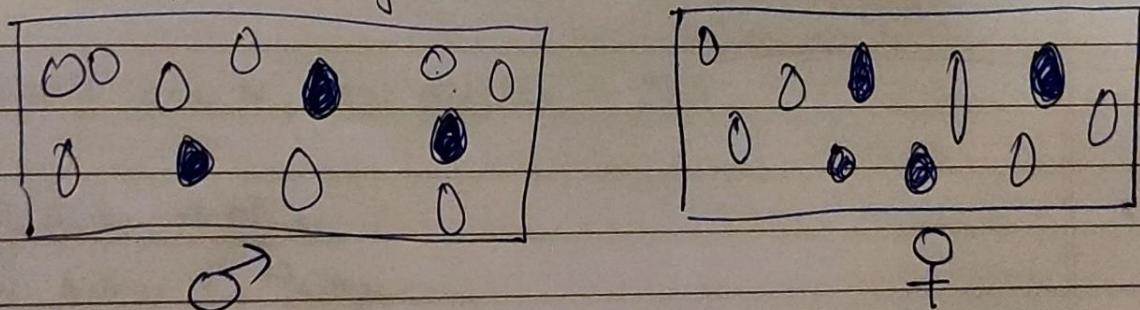
It extends mendelian laws to populations.

Example:-

Take a random population:-



At gamete level, each gamete \rightarrow 1 allele



Mating \rightarrow choose one from each box at random and combine

In this whole system, however, rest all aspects of biology are simply written off, such as behaviour, spatial etc.

Again, take 2 alleles.

Assume no. of individuals = N

Alleles $\rightarrow A_1, A_2$

\therefore Possible individuals $\rightarrow A_1A_1, A_1A_2, A_2A_2$

let frequency of $A_1 = p$

let " of $A_2 = q$

we know $p+q = 1$

Assume freq. of $A_1A_1 \rightarrow X \rightarrow N_{A_1A_1}/N$

" of $A_1A_2 \rightarrow Y \rightarrow N_{A_1A_2}/N$

" " of $A_2A_2 \rightarrow Z \rightarrow N_{A_2A_2}/N$

$$\therefore p = \frac{X+Y}{2}, q = \frac{Y+Z}{2}$$

if individuals are N , total alleles $\rightarrow 2N$

no. of $A_1A_1 \rightarrow N_{A_1A_1}$

" of $A_1A_2 \rightarrow N_{A_1A_2}$

" " of $A_2A_2 \rightarrow N_{A_2A_2}$

\therefore Total no. of A_1 alleles $\rightarrow 2N_{A_1A_1} + N_{A_1A_2}$

" " of A_2 alleles $\rightarrow N_{A_1A_2} + 2N_{A_2A_2}$

Frequency of A_1 alleles $\rightarrow \frac{2N_{A_1A_1} + N_{A_1A_2}}{2N}$

$$\rightarrow \frac{N_{A_1A_1}}{N} + \frac{1}{2} \left(\frac{N_{A_1A_2}}{N} \right)$$

$$= X + \frac{1}{2} Y$$

Deriving Hardy - Weinberg Law:-

Frequency of A_1 in parents $\rightarrow [P]$

\downarrow (Normal segregation, no migration, no mutation, equal fertility)

Frequency of A_1 in all gametes $\rightarrow [P]$

\downarrow (large populations, equal fertilizing capacity)

Frequency of A_1 in gamete forming zygotes $\rightarrow [P]$

\downarrow Random mating

\downarrow equal frequency in males and females

Genotypic frequency of zygote

So basically :-

♂

♀

from this

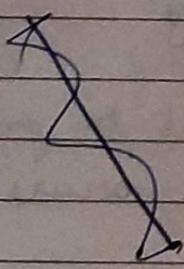
gamete pool, \rightarrow same for female :-

prob. of selecting A_1

is p and A_2 is q

♀

Now zygote:-



$A_1 A_1$	$A_1 (p)$	$A_2 (q)$
A_1	$A_1 A_1 (p^2)$	$A_1 A_2 (pq)$
A_2	$A_1 A_2 (pq)$	$A_2 A_2 (q^2)$

$A_1 A_1$

p^2

$A_1 A_2$

$2pq$

$A_2 A_2$

q^2

These are only possibilities, thus, $(p+q)^2 = 1$

Point-2 :-

The Hardy Weinberg Law:-

In a large random mating population, with no selection, mutation or migration, gene and genotypic frequencies are constant from generation to generation and there is a simple relationship between gene and genotypic frequencies.

Using H-W :-

- To determine if population is in equilibrium
- ~~except~~ compute allele (gene) frequencies
- Calculate expected genotype frequency
- compare observed number of homozygotes with expected number

(A_1A_1 , A_2A_2)

Imp. Pts. to be noted:-

- Gene, genotype frequencies do not change from generation to generation.
- Relationship between gene and genotype is reached in one generation itself
- Progeny gene frequency depends on PARENT gene frequency NOT genotype frequency
- Frequency of heterozygotes (A_1A_2) can't be greater than .5, this ~~maximum~~ maximum occurs when $P = q = .5$
- If gene frequency is low, the rare allele is mainly seen in heterozygote.
- Neutrally stable equilibrium

Extension of H-W equilibrium to multiple alleles:-
 $(p_1 + p_2 + \dots + p_n) \xrightarrow{②}$ because population is diploid.

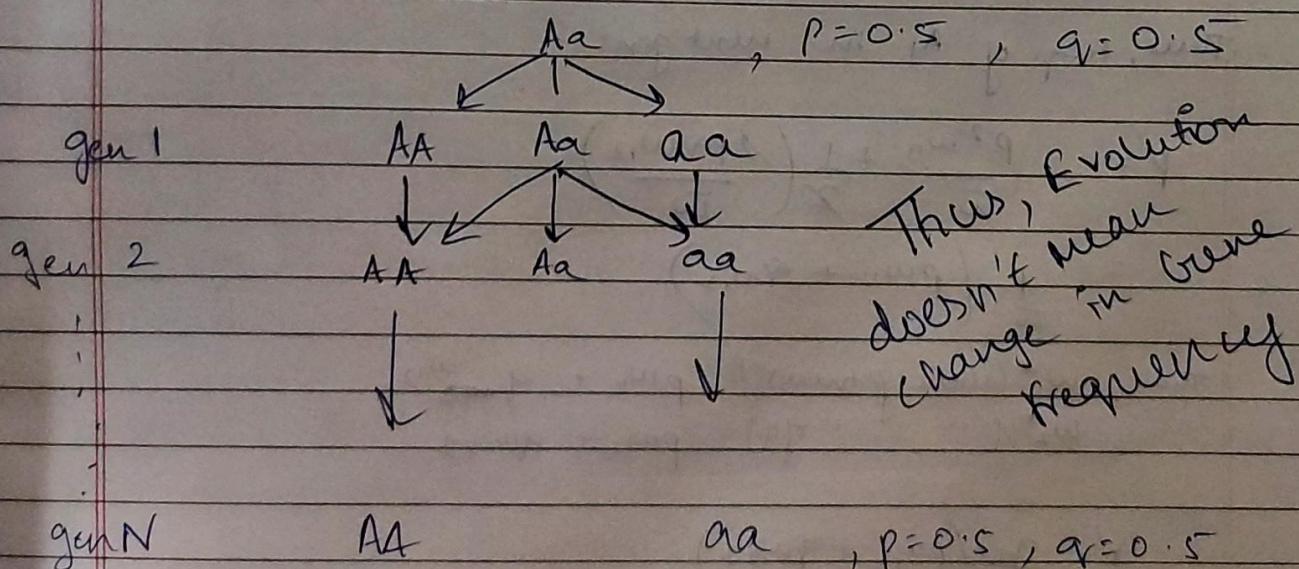
Why is H-W equilibrium imp.:-

- One of the few LAWS in bio
- Asserts that, all else being equal, allelic diversity is maintained
- Provided strong support for Darwin's evolution theory
- Expands easily to multiple loci
- Helps in calculating the gene frequency of the ~~recessive~~ recessive allele and the Frequency of carriers in a population.

CHAPTER-II :-

Part I :-

Take a population starting with Aa



The final population looks completely different from original population (genotypically). Yet, gene frequency remains same.

11 Population Genetics

Extension of H-W equilibrium to multiple alleles :-
 $(p+q+\dots+m)^2 \rightarrow$ because population is diploid.

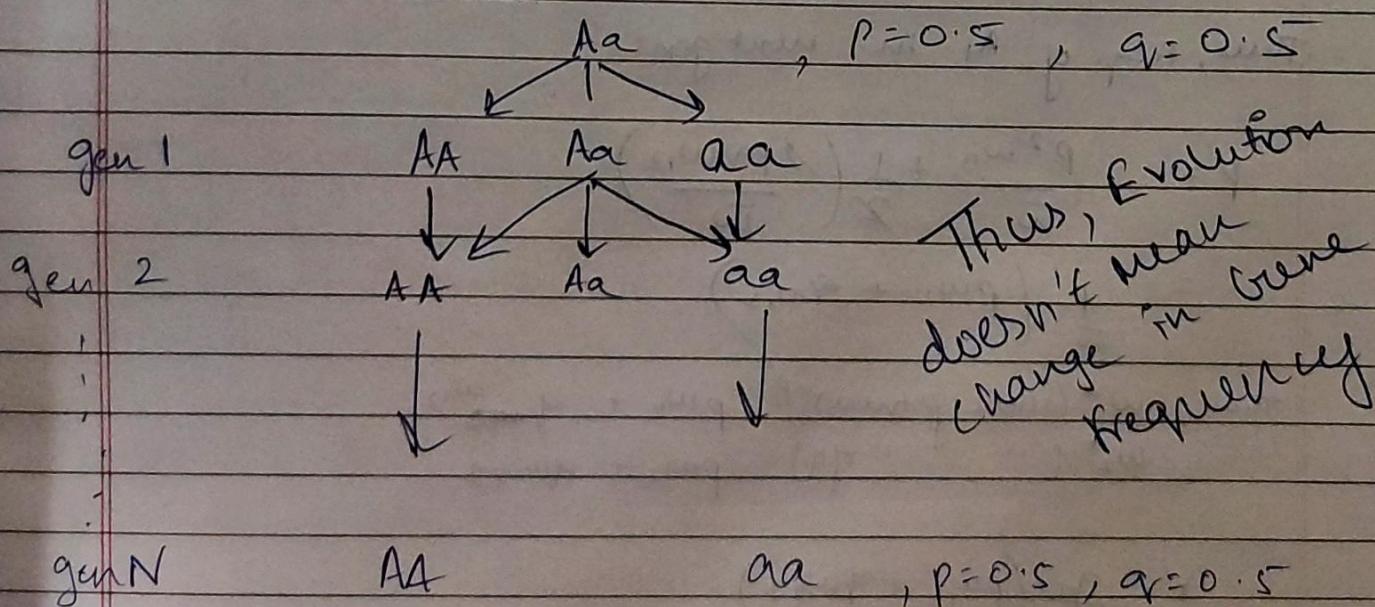
Why is H-W equilibrium imp. ? -

- One of the few LAWS in bio
- Asserts that, all else being equal, allelic diversity is maintained
- Provided strong support for Darwin's evolution theory
- Expands easily to multiple loci
- Helps in calculating the gene frequency of the ~~recessive~~ recessive allele and the frequency of carriers in a population.

CHAPTER-11 :-

Part 1:-

Take a population starting with Aa



The final population looks completely different from original population (genotypically). Yet, gene frequency remains same.

Let us perform a viability selection:-

A₁, A₂

P q q = 1 - P

~~freq.~~

Genotype P² 2Pq q²
freq.

Gene fitness w₁₁ w₁₂ w₂₂

∴ avg. fitness

$$\bar{w} = p^2 w_{11} + 2pq w_{12} + q^2 w_{22}$$

∴ freq.

$$\text{after scaling} \rightarrow \frac{p^2 w_{11}}{\bar{w}}, \frac{2pq w_{12}}{\bar{w}}, \frac{q^2 w_{22}}{\bar{w}}$$

Thus, freq. of A₁ in next gen:-

$$\begin{aligned} p' &= \frac{p^2 w_{11}}{\bar{w}} + \frac{1}{2} \left(\frac{2pq w_{12}}{\bar{w}} \right) \\ &= \frac{p}{\bar{w}} (pw_{11} + qw_{12}) \end{aligned}$$

$$\begin{aligned} \text{Thus, } w_1^* \text{ (allelic fitness)} &= pw_{11} + qw_{12} \\ w_2^* \text{ (" " " q)} &= pw_{12} + qw_{22} \end{aligned}$$

$$\therefore q' = \frac{q}{\bar{w}} (pw_{12} + qw_{22})$$

$$\begin{aligned}\bar{\omega} &= p^2 \omega_{11} + 2pq\sqrt{w_{12}} + q^2 w_{22} \\ &= p^2 \omega_{11} + pq\sqrt{w_{12}} + pq\sqrt{w_{12}} + q^2 w_{22} \\ &= p(p\omega_{11} + q\sqrt{w_{12}}) + q(p\sqrt{w_{12}} + q\sqrt{w_{22}}) \\ \bar{\omega} &= p\omega_1^* + q\omega_2^*\end{aligned}$$

$$\text{Now, } \Delta p = p' - p$$

$$\begin{aligned}&= \frac{p}{\bar{\omega}} \omega_1^* - p \\ &= \frac{p}{\bar{\omega}} (\omega_1^* - \bar{\omega}) \\ &= \frac{p}{\bar{\omega}} (\omega_1^* - p\omega_1^* - q\omega_2^*) \\ &= \frac{p}{\bar{\omega}} (\omega_1^*(1-p) - q\omega_2^*) \\ &= \frac{p}{\bar{\omega}} (q\omega_1^* - q\omega_2^*) \\ &= \frac{p}{\bar{\omega}} (\omega_1^* - \omega_2^*)\end{aligned}$$

$$\text{so } \bar{\omega} = p\omega_{11} + 2pq\sqrt{w_{12}} + q^2 w_{22}$$

replace q with $(1-p)$

$$= p^2 \omega_{11} + 2pw_{12} - 2p^2 w_{12} + w_{22} + p^2 w_{22} - 2pw_{22}$$

$$\frac{d\bar{\omega}}{dp} = 2p\omega_{11} + 2w_{12} - 4pw_{12} + 2pw_{22} - 2w_{22}$$

$$= 2 [p w_{11} + w_{12} - p w_{12} - p w_{12} - w_{22} + p w_{22}]$$

$$= 2 [p w_{11} + w_{12}(1-p) - p w_{12} - w_{22}(1-p)]$$

$$= 2 [p w_{11} + q w_{12} - p w_{12} - q w_{22}]$$

$$= 2 [p w_{11} + q w_{12} - [p w_{12} + q w_{22}]]$$

$$= 2(w_1^* - w_2^*)$$

Thus, $w_1^* - w_2^* = \frac{1}{2} \frac{d\bar{w}}{dp}$

Thus,

$$\Delta p = \frac{pqr}{\bar{w}} (w_1^* - w_2^*)$$

$$= \frac{par}{\bar{w}} \frac{d\bar{w}}{dp}$$

$$= \frac{par}{2} \frac{d(\ln \bar{w})}{dp}$$

wright's equations
for fitness landscape.

pqr lie between 0, 1,

thus, sign of Δp is dependant on $\frac{d\bar{w}}{dp}$

$$\frac{d\bar{w}}{dp} = 2[p w_{11} + q w_{12} - p w_{12} - q w_{22}]$$

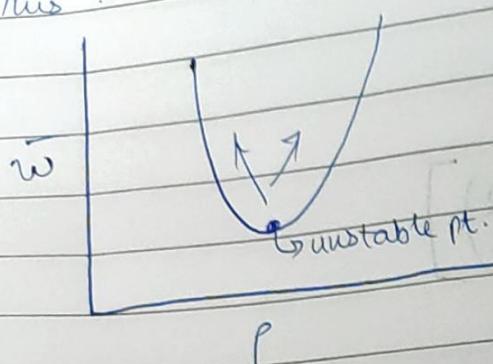
$$\frac{d^2\bar{w}}{dp^2} = 2[w_{11} - w_{12}]$$

$$\frac{d\bar{w}}{dp} = 2pw_{11} + 2w_{12} - 4pw_{12} - 2w_{22} + 2pw_{22}$$

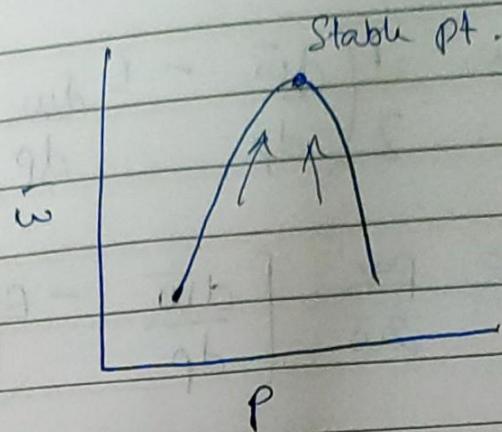
$$\frac{d^2\bar{w}}{dp^2}$$

$$\frac{d^2\bar{w}}{dp^2} = 2(w_{11} - 2w_{12} + w_{22})$$

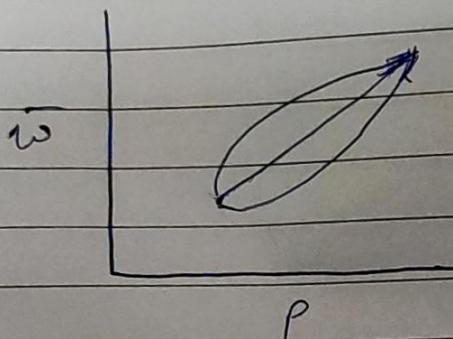
This :-



$w_{11}, w_{22} > w_{12}$
underdominance



$w_{11}, w_{22} < w_{12}$
overdominance



In all this, we have assumed fitness is frequency independent.

Part - 2 :-

Now assume frequency dependant genotypic ~~for~~ fitness

$$\frac{d\bar{w}}{dp} = 2(w_1^* - w_2^*) + p^2 \frac{dw_{11}}{dp} + 2pq \frac{dw_{12}}{dp} + q^2 \frac{dw_{22}}{dp}$$

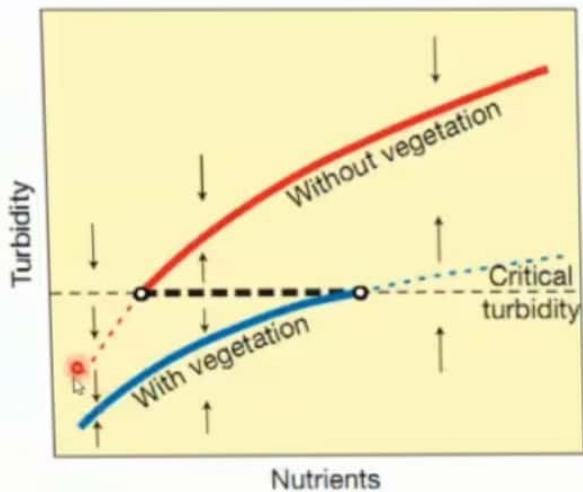
$$\Rightarrow \frac{d\bar{w}}{dp} = 2(w_1^* - w_2^*) + \left(E\left(\frac{d\bar{w}}{dp}\right) \right) \rightarrow \begin{array}{l} \text{expectation value} \\ \text{of } \frac{d\bar{w}}{dp} \end{array}$$

Thus,

$$\omega_1^* - \omega_2^* = \frac{1}{2} \left(\frac{d\bar{\omega}}{dp} - E \left(\frac{dw}{dp} \right) \right)$$

$$\therefore \Delta p = \frac{p_{av}}{2\bar{\omega}} \left[\frac{d\bar{\omega}}{dp} - E \left(\frac{dw}{dp} \right) \right]$$

12 Extra Part



A simple model for alternative stable states in shallow lakes.

Figure 5 A graphical model⁶⁰ of alternative stable states in shallow lakes on the basis of three assumptions: (1) turbidity of the water increases with the nutrient level; (2) submerged vegetation reduces turbidity; and (3) vegetation disappears when a critical turbidity is exceeded. In view of the first two assumptions, equilibrium turbidity can be drawn as two different functions of the nutrient level: one for a vegetation-dominated situation, and one for an unvegetated situation. Above a critical turbidity, vegetation will be absent, in which case the upper equilibrium line is the relevant one; below this turbidity the lower equilibrium curve applies. As a result, at lower nutrient levels, only the vegetation-dominated equilibrium exists, whereas at the highest nutrient levels, there is only an unvegetated equilibrium. Over a range of intermediate nutrient levels, two alternative equilibria exist: one with vegetation, and a more turbid one without vegetation, separated by a (dashed) unstable equilibrium.

Scheffer et al, Nature, 2001

Modern Synthesis (1950s)....

"The major tenets of the evolutionary synthesis were:

that populations contain ***genetic variation*** that arises by ***random mutation*** and ***recombination***; **UPDATE: TRUE BUT THERE ARE OTHER SOURCES OF VARIATION.**

that populations evolve by ***changes in gene frequency*** brought about by ***random genetic drift, gene flow, and natural selection;***

that most ***adaptive genetic variants*** have ***individually slight phenotypic effects*** so that ***phenotypic changes are gradual;*** **UPDATE: NOT NECESSARILY.**

that ***diversification comes about by speciation,*** which normally entails the gradual evolution of ***reproductive isolation*** among populations; and

that these processes, ***continued for sufficiently long,*** give rise to changes of such great magnitude as to warrant the ***designation of higher taxonomic levels.***"

UPDATE: CONTROVERSY. NOT NECESSARILY.

Futuyama



Selection is always behind

- NS changes gene frequencies in populations *after* exposure to selection.
 - Avg. size of *G. fortis* beaks changed because of changes in allelic frequencies in the population.
 - Allele frequencies shifted because big beaks were good *that year*.
- Selection cannot anticipate future changes in the environment.
 - If the environment changes too rapidly, population extinction may result.
 - Evolution is not forward-thinking; new mutations do not arise to solve problems.



Activate Windows
Go to Settings to activate Windows

Modern Evolutionary Synthesis

Concept:

The features of an organism are chiefly determined by its genes.

Implication:

Environment merely acts as an agent of selection.

Extended Evolutionary Synthesis

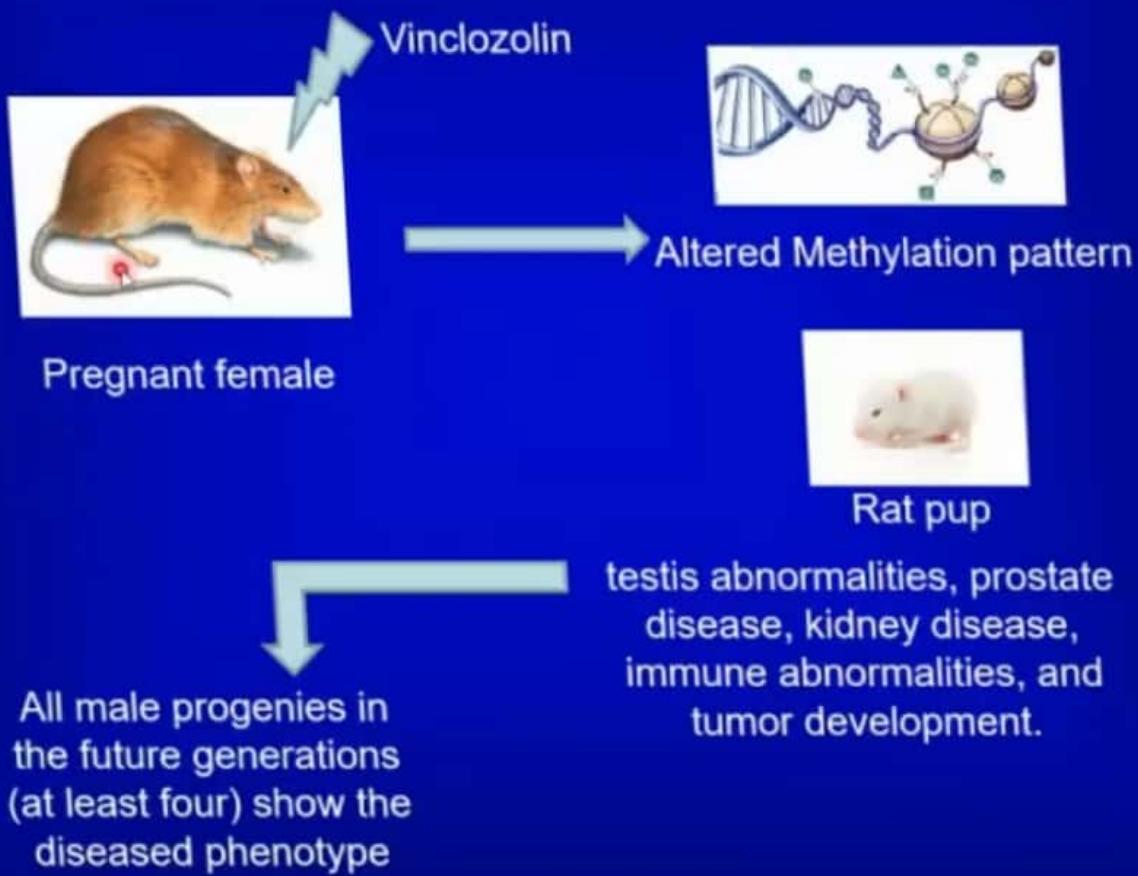
Concept:

At least some features of an organism are determined by an interaction of the gene and the epigenome.

Implication:

Environment is not a mere agent of selection, but can also directly alter the epigenome, and hence the features, of the organism.

Transgenerational Epigenetic Inheritance



Modern Evolutionary Synthesis

Concept:
Acquired traits can not be inherited.

Implication:
Adaptive evolution occurs through the differential survival of competing genes.

Extended Evolutionary Synthesis

Concept:
Some acquired traits can be inherited.

Implication:
Adaptive evolution can potentially occur at the level of both genome and epigenome.

Modern Evolutionary Synthesis

Concept:

All genetic information is passed
within the same species.

Implication:
Descent (with modification)
forming a lineage



http://www.consortium.com/pdf/magnusson_antibiology_3.pdf

Extended Evolutionary Synthesis

Concept:

Genetic information can be passed
across species.

Implication:
Descent (with modification) but
lineage is not well-defined.

