

# B13184 - ECOLOGY I

Office hours : Friday 11 am - 12 pm

## Lecture 01

What is ecology?

Greek root : Oikos

Word coined by Ernst Haeckel (1869)

Ecology - study of organisms in relationship with its environment

- study of relationship b/w organisms & environment

- scientific study of distribution and abundance of organisms [Anderson & Birch 1954]

[Odum 1971] - study of ecosystems (includes abiotic factors and environment as a whole).

Modern definition - Jonathan Krebs 1972

"Ecology is the scientific study of processes regulating the distribution and abundance of organisms, and the interactions among them, & the study of how these organisms in turn mediate the transport and transformation of energy and matter in the biosphere (i.e. the study of ecosystem structure and function)."

Why focus on regulating processes?

- \* helps us understand the why the pattern is the way it is
- \* help us quantify its stability, change etc based on the underlying processes
- \* gives us the predictive power to predict the distribution of organisms in other areas.

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## Lecture 02

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### Word association game

'Oikos' means household/environment. So ecology was coined as a term to associate with the study of organisms in/and their environment

Different branches of ecology

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## Lecture 03

Ecology as a subject overlaps with Environmental Sciences (physical, chemical, ECS aspects), Conservation biology (applied ecology with social components and hugely multidisciplinary) and wildlife biology (emphasis on the wildlife - manage & conserve).

Natural history - documentation of information about organisms and ecosystems  
Also involves classification & categorization of the info

## Levels of biological organisation

Ecosystem	Century	Realm of ecology
Population → Community	Year	
Organism / Individual	Day	
	Min	

Organ system

Seconds

Organ

Milliseconds

Tissue

Microseconds

Cell

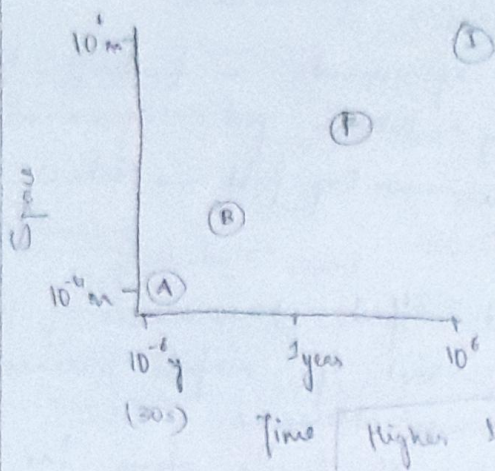
Nanoseconds

Subcellular

Molecular

If doesn't make sense to keep track of all nested levels - too many moving parts and gets too complicated.  
But they are studied in a specific context

# Scales of and patterns & processes in ecology



- A: CO<sub>2</sub> transport in leaves
- B: Nutrient transport in soil
- F: Population dynamics
- I: Climate change, paleoecology

Levels of Organisation  
 (1) Individual (2) Population (3) Community  
 (4) Ecosystem  
 Questions/Aspects that can be studied  
 Higher levels - landscape, Biome, Biosphere

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## Lecture 04

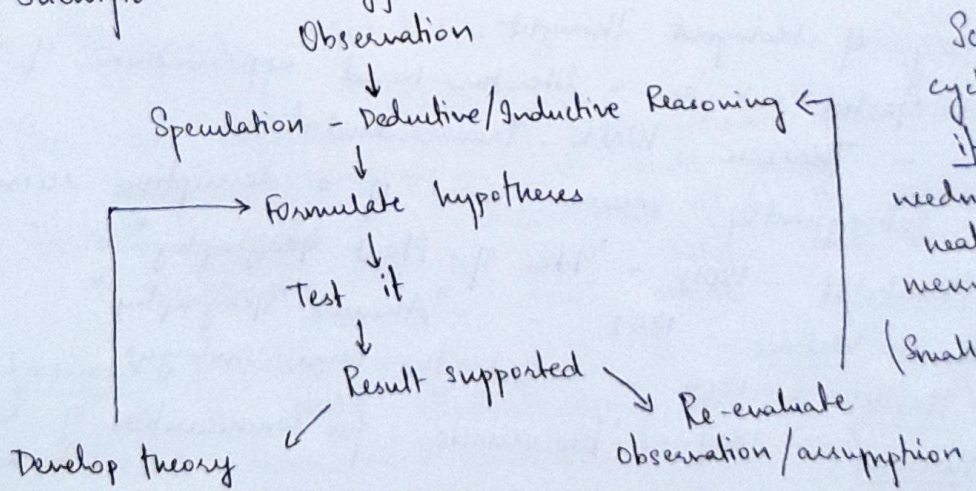
### Philosophy of Science of Ecology

Science - the approach to understanding the world around us

method of generating knowledge  
 It's based on credible, testable (verifiable),  
repeatable & evidence

- Cornerstone of scientific method -
1. Pattern - relationship b/w entities
  2. Process - how the patterns arise
  3. Theory -

### Scientific methodology



Science is cyclical and iterative but needn't be this neat - its messy & loopy (Small Pond Science)

## Experiments

Crucial component of scientific methodology → treatment group

\* - Francis Bacon: controlled in experiments, the idea of how experiments should be done

- Fisherian (RA Fisher) - analysis of variance

\* Manipulative or controlled experiments — tradeoff b/w control vs generality. Where you experiment matters — Lab → Greenhouse → Exp field → Natural field

\* Natural observational experiments

Eg: How rainfall gradient affects performance of plants? From Pune → Kerala, amt of rainfall increases and the dry season decreases.

Studying the productivity of forests along the precipitation gradient is like an experiment but it's actually a natural phenomenon.

These are called observational experiments.

Useful for large spatial & temporal scale

Drawbacks: harder to prove causality

there are too many variables between natural study sites. 'All other factors' can't be controlled for.

\* Natural experiments: similar to obs experiments but here what is being observed is a chance occurrence and studying how it affects what the focal

## History of Ecological Thought

• It started out as a literature-based appreciation of nature — Thoreau, Waldo, Transcendentalism

• It subsequently became more of a descriptive science —

Thunberg - 1804 - "Idea of Plant Geography"

Russell Wallace - 1852 - "Animal Geography"

Haeckel - 1865 - coined the term 'ecology'

Möbius - 1867 - 'biocoenosis': for communities of living beings

Darwin - all patterns in nature as evolution by natural selection

Eugene Warming (early 20th cent) - founding father of ecology  
Sought to explain distribution & biogeography of plants based on morphology & anatomy.

Tansley - first experimental studies, studying competition in plants

Fisher - more experimental

Odum & Odum - 1950s - father-son duo  
Von Frisch, Tinbergen, Lorenz - 1973 - Nobel in medicine for behavioral ecology

Dobzhansky - Ecological genetics

Vincent et al. - molecular ecology - allelochemical of an invasive plant that suppressed germination & took over other plant grasslands.

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Lecture 05

Complexity in biology

This makes it hard to apply the scientific method evenly

This arises due to -

- inherent variation → multiple components & multiple factors
- modularity :: its at a higher level of organisation
- large spatial scale and temporal scale - dynamic processes
- history - most subjects of study are historical
- heterogeneity - distribution of the numerous components

There are different levels of organisations and there are complex phenomenon at each level.

Bastbolome quote : ... each level finds its explanation of mechanism in the levels below, and its significance in the levels above

Emergent properties - the whole is greater than the sum of its parts - Understanding the function of parts doesn't mean we'll understand the system

⑥

Also complexity is affected by -

- Variation in physical environment
- Stochasticity
- Inherent variation in nature
- Historical dependence - starting conditions matter

Problems and conceptual issues with ecological research  
Massimo Pigliucci 2002.

Dealing with complexity

1. Careful experimental design
2. Rigorous statistics
3. Large scale in experimentation - time & space
4. Large sample size to detect higher order interaction
5. Independent validation
6. Manipulative experiments to complement natural & observational
7. Strong inference approach - multiple alternative hypotheses, sequential orthogonal (mutually exclusive) hypotheses, sequential testing, reiteration.
8. Use more elaborate mathematical models
9. Replication in time and space

Dealing with complexity in spatial & temporal scales  
Studies have to be representative

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### Lecture 06

Organismal level  
Study of an individual and its relations between with the environment - mostly abiotic factors

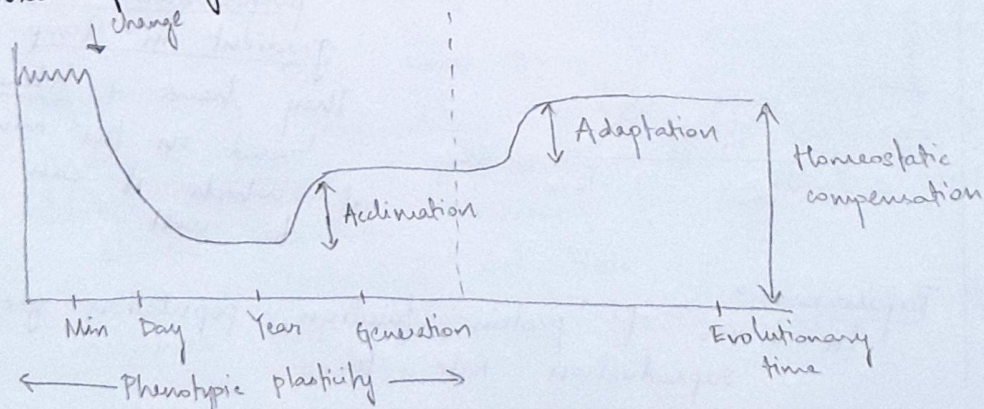
Also called physiological ecology, parts of behavioural ecology & so on

Evolution by Natural selection

- Variation in traits
  - Traits should be heritable
  - Differential fitness value / reproductive success
  - Limited resources / selection pressure : this is factored into differential fitness
- } Necessary conditions

- \* When these conditions hold, favourable traits increase in frequency over time because organisms better able to survive and reproduce leave behind more offspring.
- \* Change in the environment is not necessary but certainly helps the process of evolution along.
- \* Eg: Spread of DDT resistant mosquitoes
- \* Selection only acts on existing variation - doesn't create them
- \* Also, genetic variation is random WRT environment
- \* Whether a trait is harmful or beneficial depends on the environmental context.
- \* Evolution is the explanation for the existing patterns of abundance. So it is important aspect of ecological studies but not always.
- \* Evolution acts on individuals/organisms because they express traits & face differential fitness costs.
- \* But evolution happens at the level of the population because that's where the change in gene frequency occurs.
- \* Genetic level - mutations create variation but selection acts on the phenotypic manifestation of a number of genes, and not individual genes.
- \* How does evolution affect the levels above? Species interaction, diverse communities being more stable etc

Responses of organisms to change - Acclimation vs Adaptation



Acclimation - Adaptation - they are processes through which organisms try to maintain functional level of life processes in the face of change.

They occur at different timescales.

Acclimation - phenotypic plasticity - over the lifetime

Adaptation - change through several generations.  
change in genetic make-up

### Physiological ecology

- Study of interactions b/w organism & abiotic environment

Abiotic factors - temp, water, pH, salinity, pollution, wind

- These factors can be a condition or a resource.

A resource (eg. soil nitrate) is finite and gets consumed i.e. once taken up by one organism can't be consumed by another.

Both condition and resource affect the organisms.

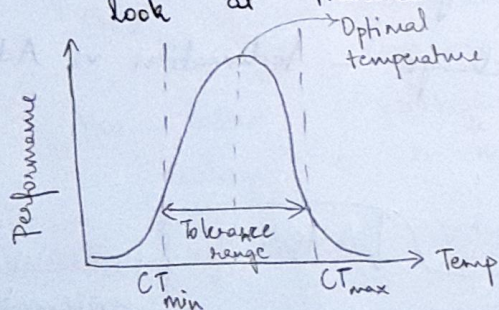
- Abiotic environment can vary on macro & micro scales

- The adaptations of organisms to abiotic conditions are fundamentally constrained

- Water: condition for aquatic organisms but a resource for terrestrial organisms.

### Niche concept

To study the effect of T on organisms, we will look at thermal niches based on performance curve



Every organism has a unimodal performance curve for a gradient in temp.

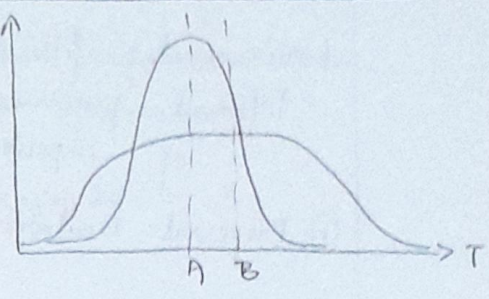
They have a tolerance range based on the min & max T at which it can survive and do well.

Performance?

In terms of protein function, population growth rate ( $r$ ), reproduction rate etc.



\* Organisms can have wider or narrower niche breadths.  
 A - specialist B - generalist  
 A generalist has a lower performance ∴ there's a cost for adopting to a wider range of temperatures.



\* Organisms are also cold-adapted or warm-adapted. If ambient T changes, their performance also changes.

This niche concept can be extended to other abiotic factors - pH, salinity etc.  
 We can have different factors in different axes and define the region where the tolerant ranges intersect as a n-dimensional volume. This represents the niche of the organism.

Niche - combination of suitable ranges of abiotic factors that allow the organism to survive, grow & reproduce

Realised niche - the actual range in which the organism thrives at the borders of fundamental lines. It can't thrive at the borders because of biotic factors (like competition, predation, disease).  
 What about slight change in condition at the edges would kill the organism?

This has been measured: Hutchinsonian niche for seahorse egg development based on O<sub>2</sub>, T, salinity.

This definition of niche was given by Hutchinson (1958) n-dimensional hypervolume where dimensions are abiotic conditions & resources. Niche defines the abiotic conditions necessary for survival & persistence

Criticism - it's a restricted definition assumes that abiotic factors are independent of one another.

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How is niche related to habitat?  
The conditions of habitat (a physical space) give us the constraints of realized niche.

### Environmental filtering

Different processes regulate the distribution and abundance of species -

① Dispersal limitations

\* + # Δ □

Regional pool

----- ↓ -----

② Habitat filtering

+ # Δ

Only those whose fundamental niche overlaps with the dispersal range

----- ↓ -----

③ Biotic interactions

+ Δ  
Community

competition, predation etc.

2/07

### Lecture of

Niche is an abstraction.

- Effects of temperature are - universal and pervasive
- The effects are felt across all scales and various levels of organisation (protein activity & growth rate)
  - Also these effects permeate through different levels.  
Molecular changes can affect physiological performance and other higher level processes.

### Variation in temp.

Spatial : Latitude - decreases poleward

Altitude - 1°C drop with 100m increase

Proximity to ocean ; Aspect - Northern vs Southern slope

Temporal : Season - time of the year

Diurnal - time of the day

Microclimate - ~~expo~~ canopy position, topography etc.

Aspect : In NH, south-facing slope receives more sunlight hence dry & less vegetation

SH, southern slopes have more vegetation

### Homeostasis

All organisms have to deal with large fluctuation  
Regulation of internal conditions (homeostasis) is  
important to keep functioning well.  
This regulation is energy expensive

### Conformers vs Regulators

Dependent on ext. conditions

Wide range of conditions

Broad but shallow performance curve

Reduced cost of homeostasis

Ectotherms - lizard ← source of heat

Independent of ext. conditions

Narrow but higher p.c.

Expend energy for homeostasis

Endotherms - Mammals

Homeotherms

Poikilotherm ← Body temp

Stenotherm (specialist)

Eurytherm (generalist) ← Niche breadth

All homeotherms are stenotherms, but the opposite is not true  
In very stable conditions, even an ectotherm can  
be a specialist.

Plants can regulate T to

Example: Skunk cabbage - Symplocarpus foetidus

This plant just before snowmelt, generates heat  
through mitochondria as a 2<sup>o</sup> process of respiration.  
So it develops, grows & blooms early - so it  
doesn't have to compete with other plants.

### Temperature & Metabolism Q10

For every 10° increase in temperature, the metabolic  
activity of enzyme increases by twofold.

But this cannot be done indefinitely - proteins denature  
at a particular enzyme

← within physiologically relevant ranges of T

## Temperature and body size

### Bergman's Rule

Body size increases with poleward latitude i.e. ↓ in temp  
Sun bear < Himalayan black bear < Brown bear < Grizzly bear < Polar bear

This relationship has been shown with other related animals - foxes, rodents  
Reason: surface area - volume ratio

### Allen's Rule

Extremities of animals decreases with increase in latitude or decrease in temperature

Eg. Hares - size of ear decreases from equator → pole  
Studies with humans - body size & weight - also showed similar trend  
Distribution of C4 grass cover (which does better at high T) also varies with temperature.

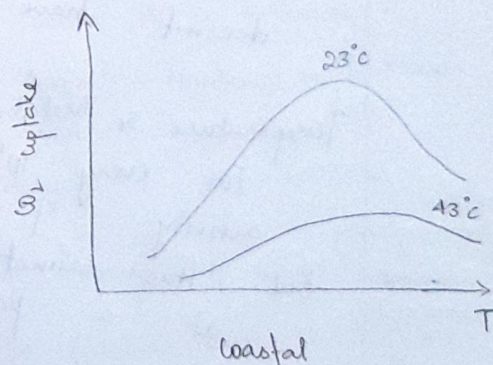
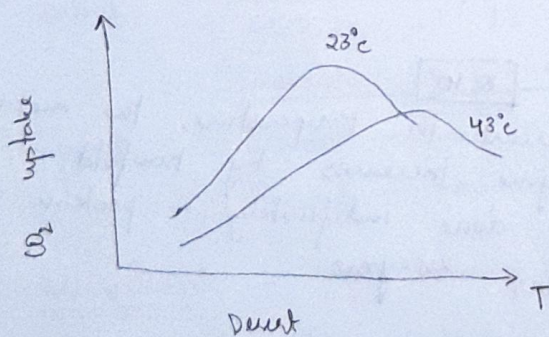
Temperature & species richness  
in Species richness and diversity decreases with decrease in temperature. So T also affects higher ecological processes.

lecture 08

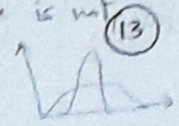
### Acclimation

Eg: Atriplex - saltbush : 2 types of populations - desert & coastal  
Borey & Bjorkman 1980

They grew two kinds of population in both high and low temp.



Then the cool grown and hot-grown plants are kept at assay temp (x-axis) and the photosynthesis rate is measured

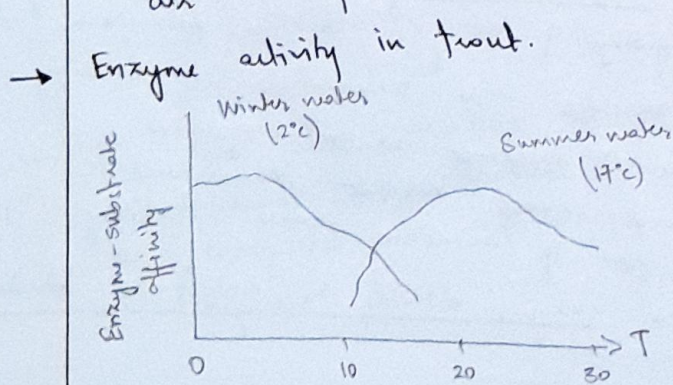
Coastal - specialist (∴ small range of T). But its performance is not greater than desert plant (generalist). (counter example of )

Need to revisit assumptions

- \* Desert plot: The optimal T of hot-grown plants is higher than cool-grown ones. After  $\approx 35^\circ\text{C}$ , the performance of cool-grown is lesser than that of hot-grown plants.
- \* Coastal plot: The cool-grown plants have similar levels of productivity as desert plants. But hot-grown coastal plants are doing quite bad in terms of performance. But the  $T_{opt}$  of hot-grown is higher than cool-grown coastal plants. So desert plants have acclimated without compromising performance. Even the coastal plants have acclimated, but not very well.
- Possibly cuz: desert population faces wide range & fluctuating temperature diurnally & seasonally. So might be easier for them to acclimate. Whereas coastal population is used to moderate & stable temp.
- So the point is that: the two populations are genetically different cuz they're adapted to their own climates. This means that even adaptability could be different - coastal population can't acclimate to desert conditions anymore.

Other factors might be important

# Measuring  $\text{CO}_2$  uptake: A quercus is clamped over the leaf and conditions in it can be controlled. The air composition inside is monitored & plotted.

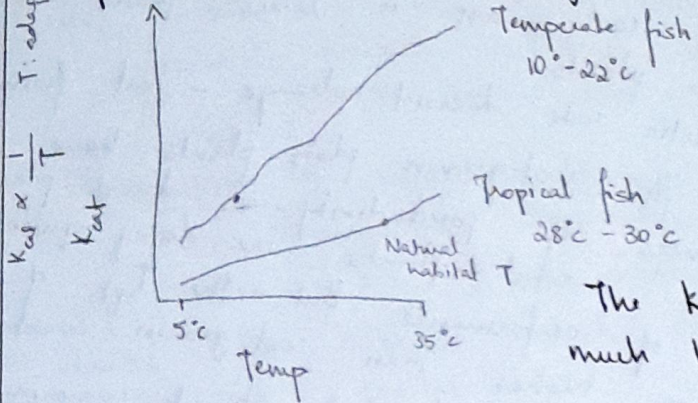


Two forms of acetylcholine-esterase were studied in trouts that were cool-adapted and warm-adapted acclimated. The optimal temp of performance shows a distinct shift.

The two curves are possible because there are two isoforms of the enzyme and based on environmental conditions, different isoforms are expressed

ALSO:  $E_a$  of ectotherms is lower than that of mammals.

### Temperature adaptation of enzymes - Somero



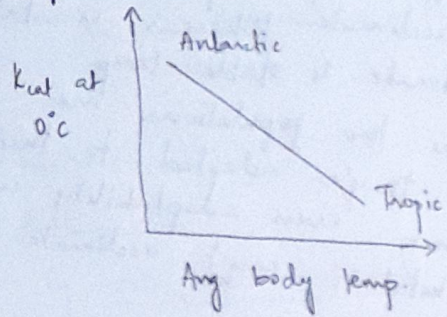
$K_{cat}$  of lactate dehydrogenase is the enzyme turnover rate - the amt. of substrate processed per unit enzyme per unit time.

The  $K_{cat}$  of temperate fish is much higher than tropical fish.

In fact, the difference is increasing as T increases.

But if we look at the graph, the  $K_{cat}$  values are similar for their native temperature

Hypothesis: compensatory adaptation of enzyme turnover rate.



That cold adapted animals have increased  $K_{cat}$  to compensate for lower reaction levels at lower temperature. So they've increased the efficiency of their enzyme.

Ultimately, enzyme activity =  $K_{cat} \times [\text{enzyme}]$

So why haven't all organisms evolved highest possible  $K_{cat}$  so that they can produce lesser amt of enzyme and save energy?

\* Usually, change in enzyme conc. is an acclimation response. Evolutionary adaptation  $\Rightarrow$  change in intrinsic properties.

Ans: George Somero in notes:  $K_{cat} \propto \text{flexibility}$ . To remain stable at that temp, the rigidity of hot > cold. This determines  $K_{cat}$ .

Also  $K_m$  ( $\propto \frac{1}{\text{affinity E-S}}$ ) increases with temperature i.e. binding affinity decreases as T increases in an organism.

$K_m$  remains conserved across habitat temperatures. i.e. the enzyme has to maintain some stability. (?)

There's a tradeoff between enzyme activity & substrate binding

# Lecture 9

Resources - light, Air, Water, Nutrients

Ultimate source of energy - sunlight

But there are other forms of energy. Microbes in deep sea vents use chemical energy ( $H_2S$ ).

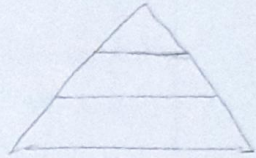
MC Escher - visual artist - his illustration shows perpetual motion machine through optical illusion. But this violates 2nd law of thermodynamics, efficiency can't be 1.

Cartoon of a biological perpetual machine - mosquito & frog

Energy flow in food web.

But there's no biological perpetual machine. At each successive trophic level, only 5-20% of usable energy is transferred from lower to higher level.

This gives rise to the biomass pyramid.



Inverted biomass pyramid has been reported in some marine systems, based on how its averaged over time & space - its actually a fallacy

Solar energy

- Only 1-2% of light is used by living beings
- $\frac{1}{3}$  is reflected by clouds
- $\frac{1}{3}$  warms sea & land
- $\frac{1}{4}$  is used up in evaporation & drives water cycle.

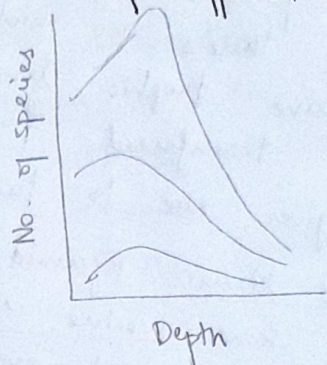
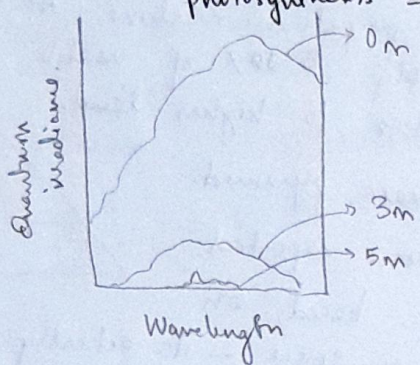
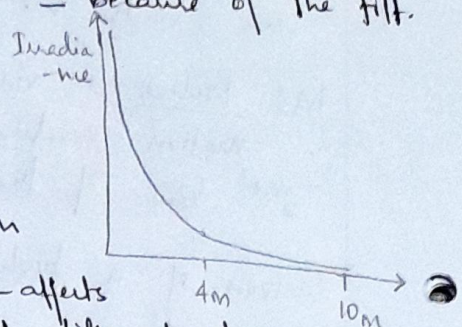
Spatial variation in availability of solar energy. This is based on the angle of incidence of light rays.

There is also variation at microspatial scales. This is very apparent in tropical forest - the forest floor gets 2% as compared to cap canopy. Its less prominent in temperate forest and agricultural fields.

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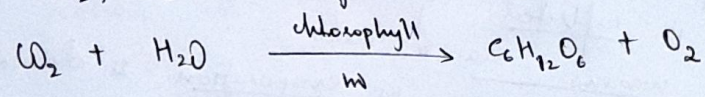
- There are also temporal variation in availability of sunlight
- In tropical regional, Sunlight is more or less constantly available throughout the year, except for monsoon  
Photoperiod & sunlight intensity also remain constant.
- Temperate region: There's an annual cycle of sunlight intensity and photoperiod based on the season. Photoperiod increases in the summer & decreases in winter months
- Polar region: exacerbated conditions of temperate region.  
6 months summer, 6 winter - because of the tilt.

- Variation of light with depth in aquatic systems.
- Qualitative variation of light at  $\lambda$  with depth.  $\rightarrow$  quality of light varies - affects photosynthesis  $\rightarrow$  distribution of different algae varies.



### Photosynthesis

A way of fixing carbon in organic molecules using  $\text{CO}_2$ ,  $\text{H}_2\text{O}$  & light energy



$\text{CO}_2$  &  $\text{O}_2$  are important for plant metabolism. So they should have an efficient exchange of gases.

In this process, the plants lose  $\text{H}_2\text{O}$  - so transpiration is a necessary evil.

Plants only have passive process to exchange gases. So they have increased surface area, which in turn makes the loss of water greater.



### More about plants -

#### → Overview of plant structure

- Parts - leaf, leaf primordia, shoot apex, node, internode, stem,  
 lateral root, tap root, root hairs, root apex
- leaves: photosynthesis
  - stem: support
  - Roots: anchorage, absorption
  - node: leaf attaches to stem

#### → The leaf

Cross-section: cuticle, upper epidermis, palisade parenchyma,  
 spongy parenchyma, xylem, phloem (veinlet),  
 lower epidermis, stomata, guard cell

#### → Plant cell

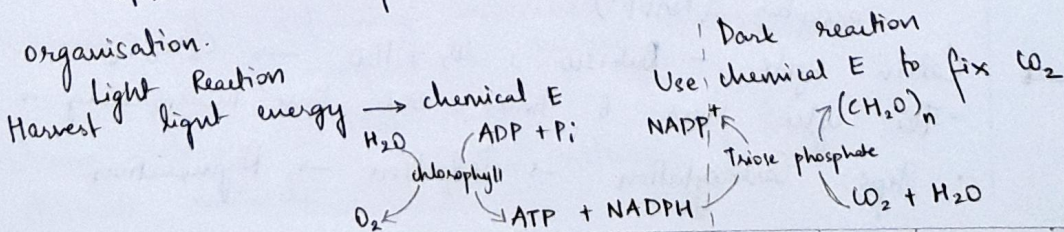
Cell wall, middle lamella, cell membrane, chloroplast,  
 mitochondria, Golgi, smooth & rough ER, nucleus,  
 vacuole, ribosomes

#### → The chloroplast

Double-membrane organelle  
 Plate-like structures called thylakoid are stacked in  
 structures called grana, which are interconnected  
 by fret lamellae

The grana are surrounded by stroma  
 There is a chemiosmotic gradient across thylakoid membrane

→ Photosynthesis is a complex process. There are specialised structures & processes at all levels of biological organisation.



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Very little of sun's radiation reaches earth surface  
Chlorophyll absorbs strongly in the blue & red portion of the spectrum  
Green light is reflected, which gives plants their colour

→ Photosynthetic pigments  
Mainly: Chlorophyll a, b But also: Xanthophyl, carotenoids.

- Structurally almost identical - a has  $-CH_3$  subgroup while b has  $-CHO$  subgroup. So they 'tune' to slightly different wavelengths

- Chlorophyll has a complex ring structure - porphyrin ring co-ordinated to central Mg atom.

The ring contains loosely bound electrons - involved in electron transitions & redox reactions of photosyn

- When chlorophyll absorbs a photon ( $\uparrow$  energy), molecule enters higher excitation state, becomes unstable & gives up heat as energy. It enters lower excited state where it can be stable for few nanoseconds  
? - This energy causes chemical rxns to occur

→ Light Reaction  
Takes place in complexes containing light harvesting antenna and photochemical reaction centers.

Antenna collects light & transfers it to the reaction centers. Chemical reactions store some energy by transferring electrons from chlorophyll to an  $e^-$  acceptor molecule

⇒ Electron Transport Chain  
A series of coupled oxidat<sup>n</sup>-reduct<sup>n</sup> rxns where  $e^-$ s are passed from one membrane-bound protein/enzyme to another before finally attached to a terminal electron acceptor ( $NADP^+$ )

⇒ Calvin cycle - Rubisco :  $CO_2 + H_2O \rightarrow C_6H_{12}O_6$   
• The cycle runs 6 times, each time incorporating a new carbon  
• Steps: Carboxylation  $\rightarrow$  Reduction  $\rightarrow$  Regeneration.

# Has Ecology Grown Up? - Grace 2019

Peter's main criticisms -

1. Questions are poorly formulated
2. No fundamental laws
3. Lack of predictive hypothesis
4. Slow progress

Methodology - citation metrics

Life stages of a discipline  
Ecology is a young science - became systematic only in 1800s, not before

Progress depends on:  
Information  
Theory  
Methods/techniques

Different disciplines may face bottlenecks because of some combination of above factors.

Complexity in Ecology  
Each discipline has its own challenges - we need tailor made approaches in each one.

- Scale
- Hierarchical levels of organisation
- connected to other disciplines

So there's a lack of general laws in ecology.

But see: Grubb (1989) and Lawton (1999)

Alternate view: Focus on case studies & don't try to generalise

## Methodology in Ecology

There's a lack of Popperian methods of hypothesis testing.  
Problems with defining hypothesis, having  $H_0$ , multiple alt.  $H$ , hypotheses may not be mutually exclusive.

Strong Inference - Platt 1964  
Alternate methods - Bayesian methods

} Refer Pignicci

Results from Grace's analysis of citations

Papers in ecology have a 'higher half-life' i.e. continue to be cited longer than 'genome biology'

Is this a case of 'tortoise & hare'?

Citation nos - Ecology - 7.4 per paper per year

Genome biology - 3.8 citation /paper /year

- \* The disciplines have different rate of growth. So information gets outdated soon, so that's why half life could be lower. Because there's no burst of knowledge. Citation papers from 5-10 years are still relevant
- \* The citation numbers are influenced by the size of the community - which influences the total no. of publications & total no. of citations.
- \* These citation numbers don't reflect the total number of papers published in the field
- \* The time-scale of studies in the fields may also influence the half-life. This is connected to the development of techniques in the discipline

laws in ecology and the lack thereof  
Too complex and a lot of exceptions. So there are no laws as such. But Darwin's theory of evolution and island biogeography are rules built on first principles that generally hold true

Maybe Bayesian approach to inference is better than frequentist approach.

Keyword search result.

'Hypothesis' 'predict' 'ecosystem' & 'landscape' - they've been used more often than 1990.

So he argues : { methodology has improved  
studies are more predictive  
studies are occurring at larger scale - so they're more appropriate.

The words chosen are representative, not a correct/perfect one. So these results need to be taken cautiously. We can see the statistical tests used and the actual scale of studies to augment this word search.

Exploring hypotheses to all available reasons that may explain any observation. In constructing  $H_0$  and  $H_a$ , we should be careful to make sure that they occupy all the space and are mutually exclusive. But in ecology, (biology in general), these conditions may not hold.

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### Lecture 11

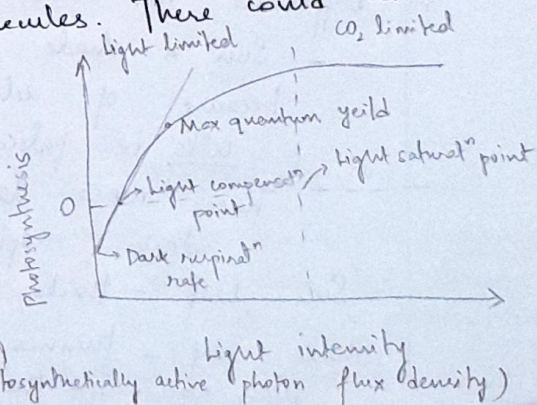
Photosynthesis - environmental effects & ecological considerations. There are different kinds of responses - passive, acclimation & adaptation.

There can be responses within a physiological range, not stress conditions.



Light # Photosynthesis is measured as  $CO_2$  uptake but not indefinitely. There is a saturation level because of biochemical constraints i.e. the electron transfer limit of chlorophyll molecules. There could also be other limiting factors.

When there's no light, plants only respire, so they give out  $CO_2$ . That's why y-axis (net  $CO_2$  uptake) is negative.  $\Rightarrow$  per unit leaf area per unit time



Light saturation point

Dark respiration rate

Light intensity (Photosynthetically active photon flux density)

Limiting factors: limitations of photosystems in reducing  $\text{NADP}^+$  limitations in rate of <sup>dark</sup> reaction  $\rightarrow$  i.e. light harvesting  
 Increased light i.e. temp in water-limited situation will make the stomata close, so  $\text{CO}_2$  uptake decreases  $\Rightarrow$  rate drops.

$\text{CO}_2$  level at high light intensity is the limiting factor ( $\approx 400 \text{ ppm}$ )

# How will increasing  $\text{CO}_2$  affect this curve?

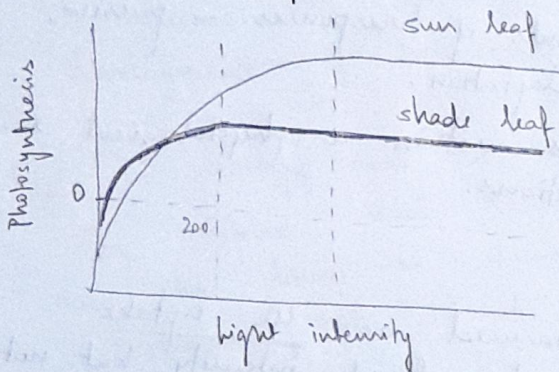
The photosynthesis rate maximum will increase and so will the light level at which the rate saturates

\* The features of the graph vary for different species

\* Quantum yield: rate of increase of photosynthesis per unit light intensity. (slope of initial curve)  $\left( \frac{\text{no. of photon}}{\text{rate of increase of photosynthesis}} \right)$

\* light compensation pt - light level where  $\text{CO}_2$  uptake =  $\text{CO}_2$  release

\* light saturation point - light level where light is no longer limiting photosynthesis. Now it's limited by  $\text{CO}_2$



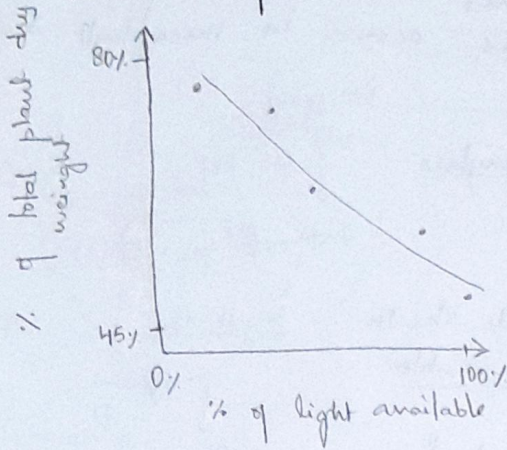
leaves of same plant, acclimated to different levels of light  
 Shade leaf is more leaf limited by  $\text{CO}_2$  after 200  
 Because of light limitations, it doesn't invest in photosystems that can process higher light levels - so shade leaf becomes  $\text{CO}_2$  limited v. quickly.

\* Difference in dark respiration rate & light compensation point  
 - Sun & shade leaves are anatomically different because of acclimation. Sun leaf is thicker, has more ~~leaf~~ cells i.e. palisade parenchyma is densely packed, has more layers. So sun leaf has higher dark respiration rate  
 - Sun leaf - thicker leaf with smaller surface area  $\rightarrow$  has more machinery  
 Shade leaf - thinner leaf with larger surface area, to optimise leaves machinery  $\leftarrow$  the chances of catching light

Keeping all else constant: Rubisco conc., temperature, water, availability etc.

## Lecture 12

## Allocation of biomass to leaves



When light is not sufficient, (low availability - limiting factor), then the amount of biomass allocated to leaves is less more.

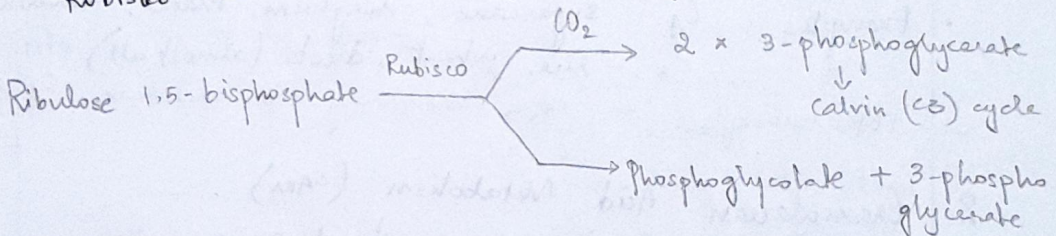
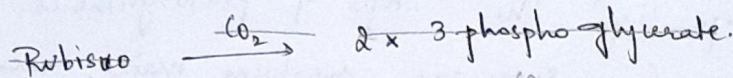
When light is not the limiting factor, biomass is invested in other organs.

## Rubisco

Most abundant protein on plant - found in plants, algae and cyanobacteria. Its used in Calvin cycle.

It catalyses the first step of photosynthesis reacts with  $\text{CO}_2$ , but also  $\text{O}_2$  - competing reactions

Rubisco

Rubisco : competing reactions

It can't discriminate well b/w  $\text{O}_2$  and  $\text{CO}_2$

In presence of high  $\text{O}_2$ , it catalyses an oxygenation reaction which leads to Photorespiration

Conditions: low  $\text{CO}_2$  / High  $\text{O}_2$  \*  
\* high temperature

Photorespiration is estimated to reduce productivity by 25%  
At high T - Ability of Rubisco to discriminate b/w  $\text{CO}_2$  &  $\text{O}_2$  worsens  
Also, when it's hot (& dry), plants close their stomata to conserve water. But they continue to photosynthesize -size  
This creates  $\uparrow \text{O}_2$  &  $\downarrow \text{CO}_2$  conditions inside the plant

(24) To avoid photorespiration, some plants have come up with alternate pathways which use a 4-carbon intermediate.

## 1. C<sub>4</sub> pathway (Hatch-Slack pathway)

It has evolved independently multiple times.

In C<sub>3</sub> plants, all processes occur in mesophyll cells

In C<sub>4</sub> plants photosynthesis occurs in mesophyll and bundle sheath cells

An extra enzyme: PEP carboxylase traps CO<sub>2</sub> and makes a C<sub>4</sub> intermediate

This is 'smuggled' into bundle sheath cells which are not permeable to CO<sub>2</sub>

In the BSC, CO<sub>2</sub> is released from 4C intermediate & goes through the usual Calvin cycle.

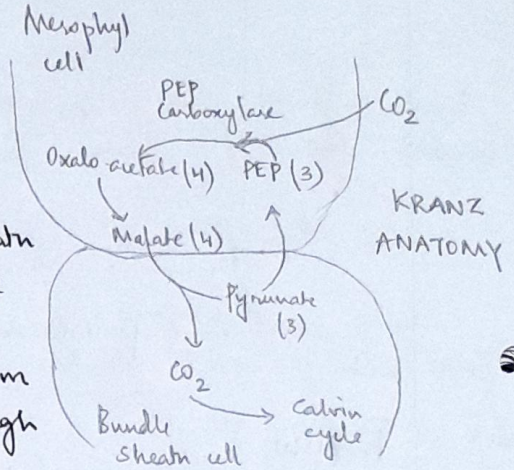
This enriches CO<sub>2</sub> in BSC & they have less O<sub>2</sub> anyway thus, PEP carboxylase doesn't have an affinity for O<sub>2</sub>.

In this way C<sub>4</sub> plants avoid photorespiration — spatially separating the steps of photosynthesis.

Examples: C<sub>4</sub>: sugarcane, sorghum, maize, amaranthus

C<sub>3</sub>: rice, wheat, dicots (almost all)

PEP carboxylase — extra machinery to maintain. C<sub>4</sub> plants pay a cost.



Kranz anatomy

## 2. Crassulacean Acid Metabolism (CAM)

CO<sub>2</sub> is fixed at night & stored as a 4C organic acid

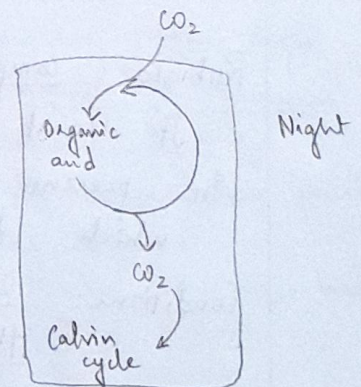
During the day, stomata is closed to prevent water loss & stored CO<sub>2</sub> is used for photosynthesis

So CO<sub>2</sub> is concentrated during the day and can be used without losing water — it can avoid photorespiration

This process separates steps temporally instead of spatially

Eg, succulents, pineapple

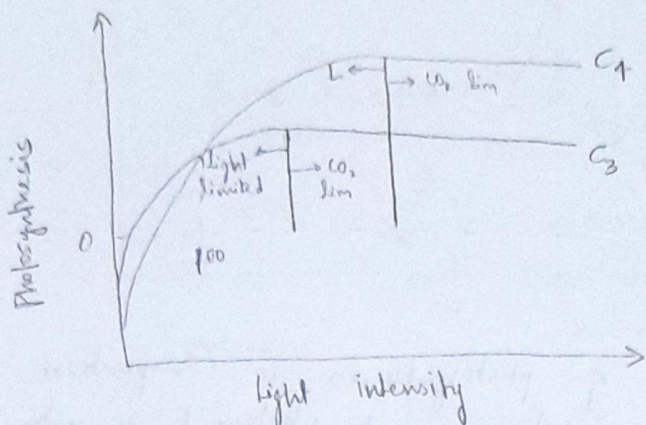
(?) — CAM can't avoid photorespiration entirely — so it's less efficient? check.





$C_4$  plants do better in hot & dry conditions. In cool & wet conditions,  $C_3$  do better cuz they don't have to make PEP-carboxylase (25)

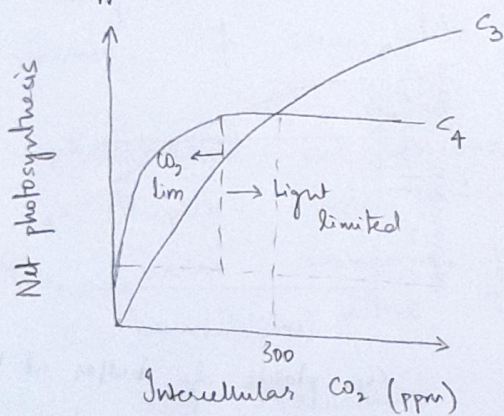
### Light response curves ( $CO_2 = 350$ ppm)



#### Discussion:

- $C_3$  plants are more limited by  $CO_2$  -  $C_4$  plants do okay  
     ↳ too much photorespiration at low  $CO_2$
- $C_4$  plants are less affected by external  $CO_2$  levels
- At low light levels (<100),  $C_3$  plants do better

### $CO_2$ effects : $C_3$ vs $C_4$ plants



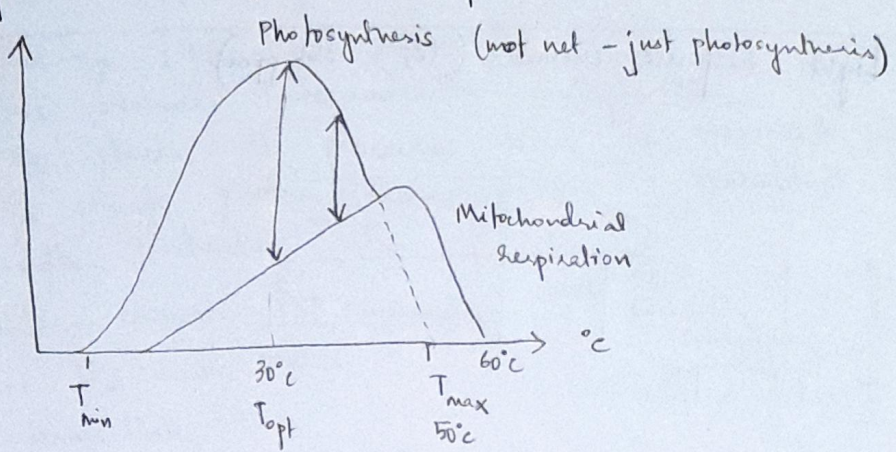
This curve is probably at light intensity  $< 200$  where  $C_3$  is doing better than  $C_4$  with increasing  $CO_2$ .

Changing light levels might shift the curves.

( $> 300$  ppm)

Very high  $CO_2$  levels -  $C_3$  plants have an advantage

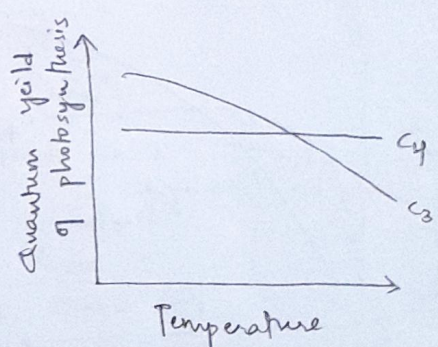
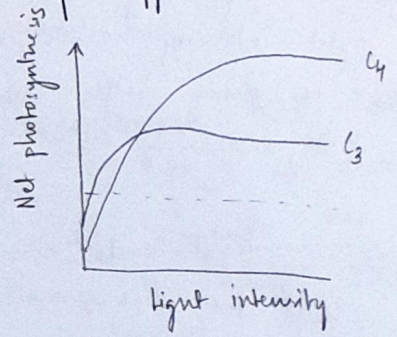
Temperature is important to plants



Differential response of photosynthesis & respiration to temperature shapes net photosynthesis with T.  
 Net p. drops with increase in T above optimal temp.  
 Also, water loss increases, photorespiration increases & enzymes degrade with increase in T.

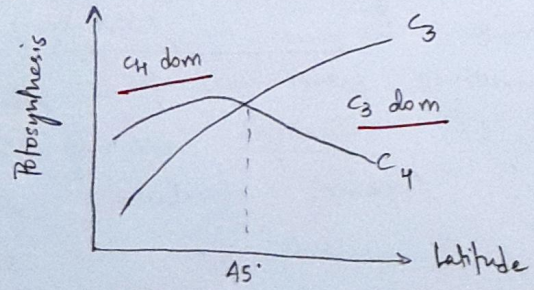
# lot of T response curves are asymmetrical - there's an increase and then a sharp drop. Usually it's not because of enzyme breakdown, but its membrane breakdown

Temp. effects: C<sub>3</sub> vs C<sub>4</sub> plants



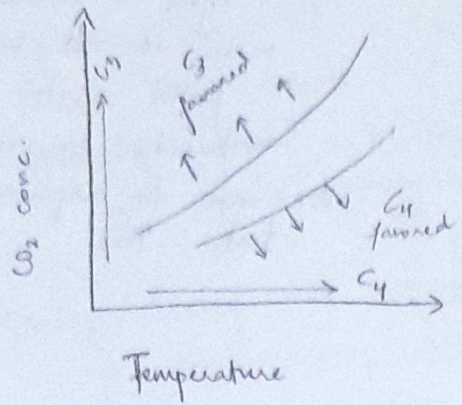
C<sub>4</sub> plants do better at higher T

Global distribution



Predictions based on T

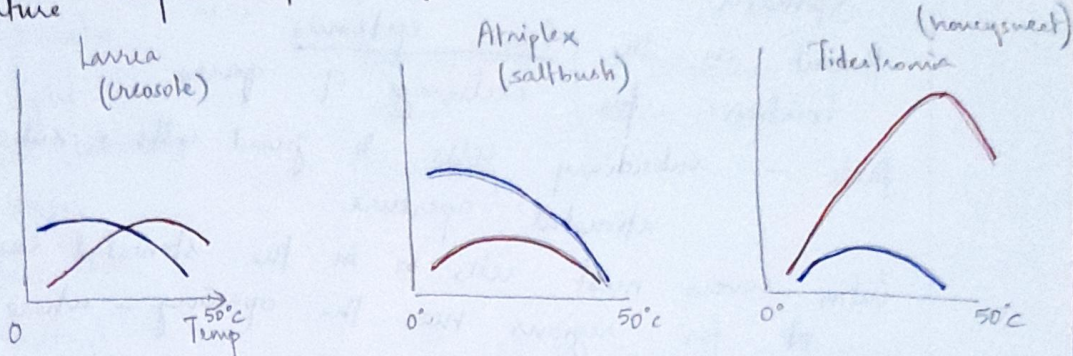
$C_3$  vs  $C_4$  distribution - based on future climate change



if they're not independent variables  
This is a simplified graph  
Increase temp & low  $CO_2$  will favor  $C_4$  plants and vice versa.  
Distribution will be affected by water, light & nutrient availability

Temperature response of photosynthesis

— cold acclimated  
— warm acclimated

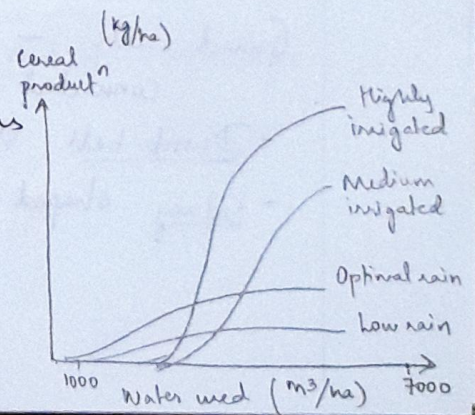


- Tidestromia & Larrea : warm-adapted - experience  $\uparrow$  temp
- Atriplex & Larrea : cold-adapted - experience  $\downarrow$  temp naturally
- Larrea - it seems like its experiences wide range of T, i.e. greater variability

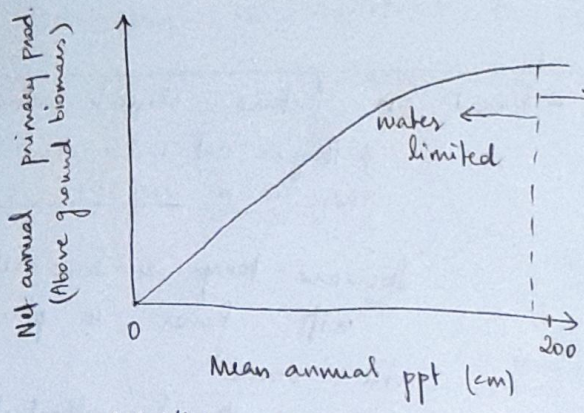
Tidestromia - hot environment } Stable surroundings.  
Atriplex - cool environment } doesn't acclimate well to hot  
Here, we're assuming that the plants can acclimate well to their native T.

Water and Nutrients

Water is limiting in agricultural systems  
This is for crops but it can be extrapolated to other plants.  
Water is a limiting resource for plants.



# Water is limiting in natural ecosystems



The rate of increase decreases with precipitation. After a certain threshold, water is not the limiting factor - its likely other nutrients or light.

We can do experiments to test this.

Whittaker 1970 - Grasslands

Quiz 2 portions -

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## Lecture 14

### Stomata

Present on the lower epidermis  
location for exchange of gases

Parts - subsidiary cells & guard cells; substomatal cavity, stomatal aperture.

Cutin covers most cells in in the stomatal cavity, except for regions near the opening - where most water loss occurs.

The closing & opening is regulated by the turgidity/flaccidity of guard cells, in turn controlled by conc of ions and water

The inner side of cell wall is thicker, so it expands differentially and stomata opens

Radial micellation - cellulose microfibrils radiate out around circumference of pore

Guard cells - only epidermal cells with chloroplasts, connected end-to-end. Types -

- Dumb-bell shaped
- Kidney shaped

### Stomatal pores

- They cover a lot of area :  $1000/\text{mm}^2$  ; 2-3% of leaf SA
- Pores are small : 14  $\mu\text{m}$  (varies)
- Optimally placed & density (sized & spaced)
  - In aquatic plants - its on the upper side
  - grasses - its on both sides of the leaf.
- Opening / closing of stomata is tightly regulated - its like a multisensory hydraulic valve

### Regulation of opening / closing -

Stomata react to -

Light

pH (internal)

Water

CO<sub>2</sub> conc.

Temperature

wind

Humidity

} Determine water loss

→ Light control  
Stomata open when light is present - because photosynthesis & gas exchange occurs.  
At night, they're closed to prevent water loss.

\* Red light - mediates indirectly through photosynthesis (a bag)  
Photosynthesis - solves energy to drive ion-pumps increases internal CO<sub>2</sub>  
Reduces pH

\* Blue light - not related to photosynthesis - directly affects guard cells  
- Activates H<sup>+</sup>-ATPase in the membrane  
- stimulates breakdown of starch & malate synthesis  
- stimulates cellular respiration.

→ Water control  
Hydropassive control - turgidity

## Hydroactive control - active mechanism

- Threshold soil water potential
- Signaling cascade initiated
- Root: ABA production
- Rapid response
- ABA signaling - downstream pathway

Why does transpiration occur?

1. Transport in plants
2. Carry nutrients in soil to the plants
3. Help in heat loss (less than air T by  $5^{\circ}-15^{\circ}\text{C}$ )
4. To maintain optimal level of turgidity.

## Root systems

Very diverse in structures. Roots acclimate based on water availability in the soil.

More water - less extensive root system - more aboveground biomass (more leaves - can afford more transpiration)  
Converse is true for less water availability.

## Plant adaptations to water

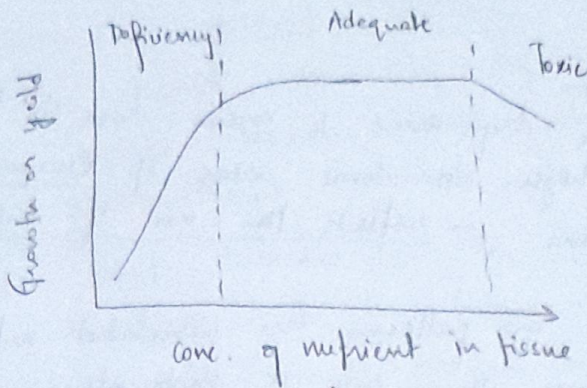
- Life history - stay dormant when water availability is low  
Eg: resurrection plant (poikilohydric)
- Deciduousness - shed leaves when water is low
- Changes in leaf morphology - lesser SA, sunken stomata, waxy layers, spines, hairs etc (more hairs: less transpiration)
- Root allocation - less water  $\Rightarrow$  increased root length, SA, increased root:shoot ratios.

# Lecture

## Mineral nutrients in plants

↳ inorganic element (mostly acquired from soil)

Nutrient: substance needed for survival



Growth is stopped after a certain level because other factors are limiting

Similar curve for crop yields with increase in nitrogen in the soil. So nutrient availability limits productivity

Nutrient use efficiency - differs for different plants

## Essential mineral nutrients -

\* **Macronutrients**: required in relatively large concentrations

↳ N, P, K, Ca, Mg, S, Si

- Nitrogen - proteins (rubisco) - usually naturally limiting
- Potassium - ion-water balance
- Phosphorus - ATP, DNA, RNA - most limiting (after N) in tropical soils
- Calcium, silicon - structurally important (Ca pectate, diatoms) grasses
- Mg - chlorophyll
- S - proteins (cysteine & methionine) - disulfide bonds

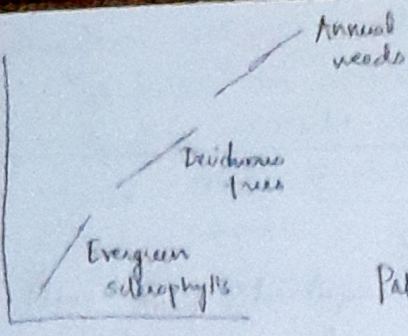
\* **Micronutrients** - required in very low concentrations

Cl, Fe, B, Mn, Na, Zn, Cu, Ni, Mo → required in least conc. & metabolism

They act as co-factors in different enzymes.

All mineral nutrients make up < 4% of plant mass, yet plant growth is very sensitive to nutrient deficiency.

Photosynthetic capacity



Needs - very fast growing  
Sclerophylls - slow growing, limited by other factors (water)

Patterns of leaf nitrogen & stomatal conductance worldwide are very similar.

Leaf Nitrogen  
→ Nardus rubica

Leaf nitrogen pattern

- It's lower in dry areas & areas close to the pole
- It's very high in some areas of Europe, India, US, China - reflects the use of fertilisers.

Stomatal conductance and patterns are correlated with leaf nitrogen through the rate of photosynthesis.

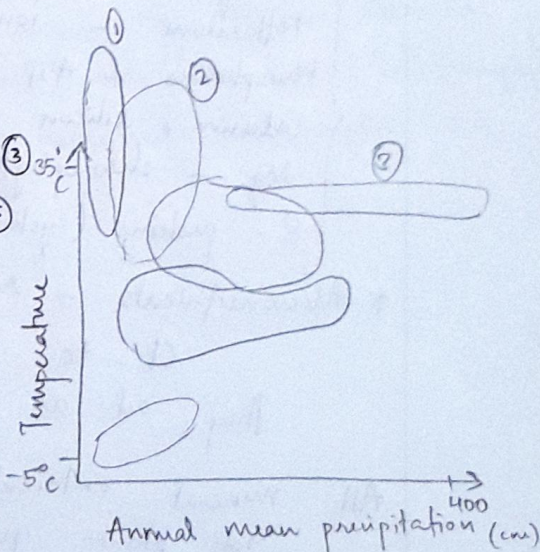
Global productivity pattern

here, Amazon is SA, equatorial forests in Africa & Indonesia etc are the most productive. US & Europe are less so.

Croplands in US & Europe are less so. This ~~is~~ doesn't match with earlier maps - this is mainly because of limitations in water (rainfall) & sunlight. It's also because US-Europe are seasonal whereas forests are constant throughout the year.

Biomes

- Desert (1), Grassland (2), Tropical forest (3)
- Temperate forest (4), Coniferous forest (5)
- Tundra (Arctic & alpine) (6)





## Global Climate change

Keeling curve - Scripps institute

In 2017,  $[CO_2] = 406$  ppm

1960  $[CO_2] = 315$  ppm

There's an annual variation in  $CO_2$  levels -  
its caused primarily by temperature - at  $T \downarrow$ ,  
 $CO_2$  uptake decreases and when temp increases,  
photosynthesis increases, so  $CO_2$  uptake increases

This rapid increase in  $CO_2$  is because of industrial  
revolution. In the future -

- Increased  $CO_2$  conc (> 800 ppm by 2100)
- Temp increase of  $3-10^\circ$  by 2100
- Increased anthropogenic  $N_2$  deposition
- Increased variability in precipitation

We need to understand photosynthetic responses to  
the rapidly changing environment - to predict  
plant responses and -

- plant productivity
- distribution
- diversity

} will ultimately affect downstream  
processes as well.

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## Pigliucci Paper (2002)

\* Nomothetic knowledge - consists of general laws to understand  
a complex nature

Idiographic knowledge - relies on descriptions of individual  
aspects of reality to reconstruct a coherent  
narrative - typical of historical sciences

\* There is a long history of criticism of 'soft' sciences  
Meehl (1978) - problems & conceptual issues

\* Higher order interactions pose strict limitations to our  
understanding of complex phenomena

- Small changes can have large impacts
- huge variation in results (lab vs wild, lab1 vs lab2)

\* the idea of mean,  
outliers etc as  
if there's an ideal  
value.

**Strong Inference (Platt 1964)**

- 1. Devise several alternate hypotheses
  - 2. Devise expts to rule them out
  - 3. Carry out expts to get as clean results as possible
  - 4. Reiterate to refine the remaining possibilities.
- Strongly tied to the idea of falsification

\* Null hyp - stats - Frequentist approach : not the best method to understand / prove a theory - not good methods

\* Bayesian inference

$$P(H_i | D) = \frac{\overset{\text{LIKELIHOOD OF DATA}}{\uparrow} P(D | H_i) \times \overset{\text{PRIOR (a priori P. of } H_i)}{\uparrow} P(H_i)}{\underbrace{P(D | H_1) \cdot P(H_1) + \dots + P(D | H_n) \cdot P(H_n)}_{\text{TOTAL P. OF DATA}}}$$

POSTERIOR P.

**Advantages -**

- 1. Multiple competing hypotheses
- 2. Question is posed in a more sensible way
- 3. Here, prob. is an estimate of degree of belief (likelihood) we are entitled to attach to a given  $H_i$
- 4. Prior - takes into account what was known of the problem before starting expt.
- 5. Gets us out of the naive dichotomy of falsification or confirmationism

Problems - \* Hard to set reasonable priors  
\* Objective vs. Subjective priors

**Somero papers**

$k_{cat} \propto \frac{1}{T}$ ,  $E_a$  follows same trend,  $[E] \propto T$  (to maintain rate)  
 $k = Ae^{-\frac{E_a}{RT}}$   $k_{cat}$  is given by  $\Delta G$  -

$\Delta H = E_a - RT$

$\Delta G = \Delta H - T\Delta S$

High  $\Delta H$  was paired with high  $\Delta S$  - enthalpy-entropy compensation  
 At a given T, cold-adapted orthologs will exist in relatively more disordered state than hot orthologs.

$\Delta S_{\text{rabbit}} = -13$        $\Delta S_{\text{bird}} = -2$

But  $\Delta H_{\text{cold}} < \Delta H_{\text{hot}}$  & the interspecific difference of  $\Delta H > T\Delta S$   
 $\therefore \Delta G$  of reaction catalysed by cold-adapted enzyme will be lower

### Lecture

Premise of the study

By varying different parameters - light intensity, T - they tried to find if C<sub>3</sub> or C<sub>4</sub> plants are more efficient in the given conditions, which might lead to the current distribution.

- C<sub>4</sub> plants need not always dominate the landscape -
- at all conditions because of intrinsic cost
- maybe they haven't had enough evolutionary time to dominate

- C<sub>4</sub> plants do the same at all temperatures - same quantum yield. But C<sub>3</sub> plants' (which do better than C<sub>4</sub> at cooler temp) quantum yield decreases with T.

# They're extrapolating this from 2 plants to all plants. Decreases with T because - Rubisco becomes less efficient. Stomata close, so relative conc. of O<sub>2</sub> increases.

- Leaf area index (LAI) - in the noon overhead sun, if the area of leaf is the same, then LAI = 1. area of shadow cast by leaf

- LAI = 1 => absolutely no shading
- LAI = 8 => self-shaded leaves => lower leaves are light-limited

Increased LAI simply means more numbers of leaves.

Fig 3 - Daily C gain vs LAI  
 For 10°/5°C - C gain increases with LAI  
 Rate of increase is larger for C<sub>3</sub> than C<sub>4</sub>  
 Also, the rate of increase slows & stabilizes

In A, at low LAI, plants are more limited by light / T but at higher LAI, it's more light limited

In B (30°/15° C) -

- \* C<sub>4</sub> plants are more efficient than C<sub>3</sub> ∴ higher T.
- \* here, the curve is qualitatively different. After LAI = 6, the net C gain decreases because p leaves are light limited, & respire more.

In C (40°/20°) -

- \* The optimal LAI has decreased - decreases with T.
- \* C<sub>3</sub> plant is doing worse because of photorespiration

Study Fig. 4 and Fig 6.

- Latitude :
- < 45° N - C<sub>4</sub> plants have an advantage
  - > 45° N - C<sub>3</sub> plants have a competitive advantage

The data in this study (photosynthetic rate) is at the sub-organelles, they calculate <sup>ε quantum yield</sup> daily C gain, individual level and they make inferences at the community level.

## Part II

### Population Ecology

↳ group of individuals of the same species that live in a particular area & interact, interbreed

Pop ecology -

1. How biotic & abiotic factors influence populations
2. Vitality of population
3. How populations evolve as natural selection acts on them

Population size:

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

Determining the individuals: to count  
Are all individuals of a species identical?

- Unitary - determinate - higher organisms
- Modular - indeterminate - eg. plants, trees, sea fan
  - \* growth forms - grasses form new individuals through nodes.
  - \* size
  - \* senescence
  - \* integration in modular organisms

Determining population size -

1. Quadrants / transects - for plants in a region
2. Mark - recapture
3. Index of abundance

Mark recapture: Survey 1 - M = 12      Total N  
 Survey 2 - C = 15      sox marked individuals  
    R = 4      are  $\frac{4}{15}$

$$\Rightarrow \frac{M}{N} = \frac{R}{C}$$

Drawbacks

- Population is not closed
- Marked animals are more/less likely to be trapped we overestimate the population
- Marked animals can die
- Marks can fall off

trapping can be traumatic - less likely  
baiting - more likely

↑

M-R methods - Peterson, Schnabel - closed pop  
Jolly - open pop modification

Bamboo - semelparous - synchronous flowering -  
masting - one event - to years - intervals  
change of cross fertilization

Life history of individual describes the stages that organisms go through -

Birth - growth - reproduction - death

Life history is the study of patterns of allocation of time & energy resources to fundamental activities such as growth, reproduction and maintenance

Life history components contribute to an individual's fitness. Different components -

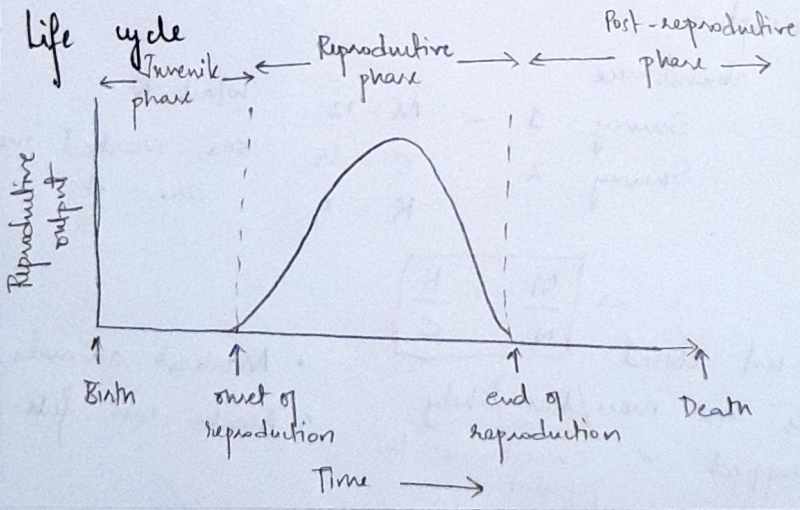
- 1. Growth & development rates and schedules
- 2. Timing of reproduction
- 3. Size at birth or germination
- 4. No. & size of offspring
- 5. Age at death
- 6. Dispersal

Nat. Sel should ideally select for organisms that start reproducing early, produce lots of high quality offspring and live forever.

Another eg: Arabidaurus

# Semelparity & synchronicity - predator satiation

BVT: Energy and resources are limited!  
Energy-resources used for one function can't be used for others => there are trade-offs



Juvenile - dominated phase by growth.

# Life cycles Annuals vs perennials

Iteroparity - multiple reproductive cycles over the course of its lifetime. Eg: humans, trees

Semelparity - a single reproductive episode before death

## → Annuals

Life cycle < 12 months

Discrete, non-overlapping generations

May overwinter as non-seed/egg

Eg: insects, butterflies, grasses

## → Semelparous

- Invests large amt. of energy in reproduction

- Adaptation to unpredictable climatic conditions are rare

- Suitable breeding grounds/conditions are low - invest everything

- Chances of reproducing again are low - invest everything in a single bout of reproduction

- Eg. Agave (century plant), bamboo, sock-eye salmon (from Pacific ocean to mountain streams - 600km)

## → Iteroparous

• Invests lesser proportion of resources in reproduction

• They have good prospects of reproducing in the future

• Its characteristic of larger organisms and those that experience more stable environmental conditions

Two factors that influence reproductive strategy -

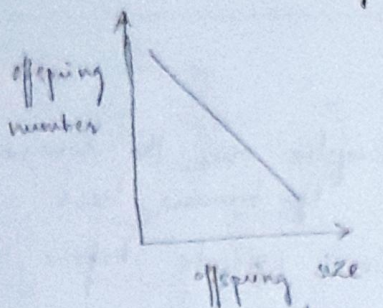
1. Prob. of offspring survival
2. Prob that adults will survive to reproduce again

Both probabilities are low in harsh conditions, so semelparity will be favoured.

Seems too much of a generalisation.

# Fecundity

There's a trade-off b/w number and quality of offspring



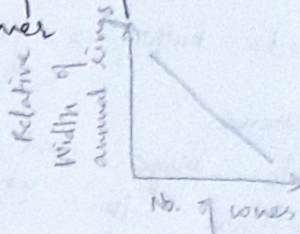
Eg. animals, pine trees  
one function, then other functions is reduced.

## Reproductive trade-offs

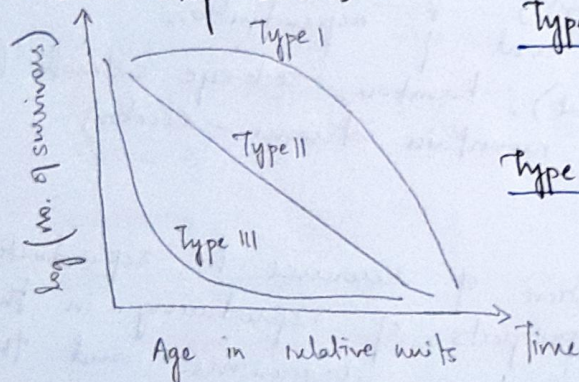
- a) Reproduction vs. future survival
- b) Reproduction vs. future growth
- c) Current vs. future reproduction

It's a zero-sum game - Principle of Allocation: if energy is used for one function, then energy available for other is reduced.

- a) Winter mortality is higher for female deer that reproduced that summer
- b) Rep vs. growth - pine tree



## Survivorship curves



Depicts proportion of population that remains alive at various points in life

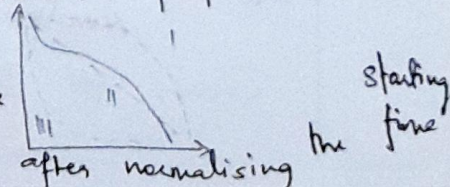
Type I - low mortality in early life, mortality conc in older age  
Eg. Humans

Type II - constant rate of mortality through life  
Eg. birds, deer, rabbits

Type III - high early mortality survivors have little mortality until old age  
Eg. plants, fish

before - 22/10/2021

Survivorship of early humans was somewhere between type I and II. Early humans had greater juvenile mortality and smaller lifespan  
Survivorship curves are generated using cohorts. For organisms that reproduce irregularly, you use different individuals after normalising the starting time





Life history space  
 If we plot Fecundity, age of maturity and Juvenile survivorship we can discuss the life history ecological strategies that these organisms adopt.

Fish have the broadest range of life history strategies whereas mammals show least variation.

Mammals - low fecundity, high juvenile survivorship, and a range of age of maturity, and a range of age of maturity, and a range of age of maturity.

Greater the investment in offspring, lower the fecundity.  
 ↑ quality ⇒ ↓ quantity.

- The different strategies give rise to -
- \* r-selected populations
    - Unpredictable/short life span
    - Density independent growth
    - large reproductive output
    - high juvenile mortality
    - Semelparity
  - \* K-selected populations
    - longer lifespan
    - Density dependent selection
    - Intense competition
    - Selection to increase adult survival
    - Decreased fecundity
    - large size
    - Iteroparity

Why do organisms age & die?  
 Senescence - late life decline in an individual's fertility and probability of survival

Causes of - bird, reindeer, drosophila.  
 Senescence ultimately leads to death. But why does it happen?

→ Possum example

Life span : 2-4 years	Energy used for:
1-3 mo : dependent on mother	1-10 mo : growth, metabolism, repair
10 mo : maturity	10-20 mo : reproduction, metabolism, repair
~ 24 mo : death (killed by predator)	

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## Rate of Living Theory

- Ageing caused by accumulation of irreparable damage to cells and tissues
- Caused by replication errors and accumulation of toxic metabolic byproducts (e.g. free radicals)
- This theory predicts that -
  1. Ageing is correlated with metabolic rate
  2. Species shouldn't be able to evolve longer lifespan
- But: no strong correlation b/w ageing & metabolic rate  
Across a wide range of organisms, 'some' correlation maybe observed.
- Another contradiction: organisms can evolve longer lifespan.

## → Evolutionary hypotheses of aging

### \* Antagonistic pleiotropy

There's a trade-off between reproduction early in life and survivorship late in life

### \* Accumulation of deleterious mutations

Over evolutionary time, mutations that are deleterious late in life can accumulate in a population

The later in life deleterious mutations exert their influence, the less likely they are to affect fitness.

Eg. diseases like Alzheimer's, Parkinson's and some cancers (have genetic basis) affect people only later in their life - so these deleterious mutations are not weeded out - they accumulate in the population.

27/10

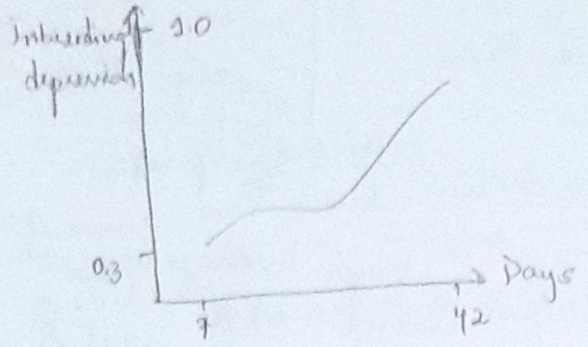
## Lecture 19

Rate of living - occurs over the lifetime of an organism

Mutation accumulation theory - here the mutations accumulate over several generations, occur only in germline cells over evolutionary timescales.

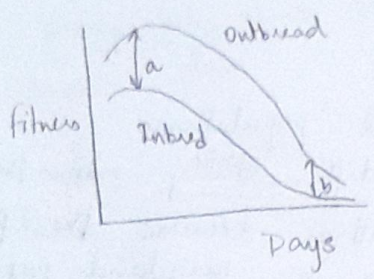
### Evidence for MAT

Inbreeding depression - crossing genetically closely related individuals leads to increased homozygosity of recessive alleles.



Inbred dep. is measured by calculating the ratio of  $\log\left(\frac{\text{inbred survival}}{\text{outbred survival}}\right)$

If inbred dep = 1  $\Rightarrow$  no flies are alive by day 42



The difference in fitness b/w inbred and outbred increases with age

$b > a$   
The fitness is worse for older flies, because deleterious mutations accumulate by them

Because of this result, it can be argued that deleterious mutations are present in the population, but manifest at old age

### Antagonistic pleiotropy

GC Williams - 1957.

Alleles that increase fitness in old age

fitness in early life but decrease

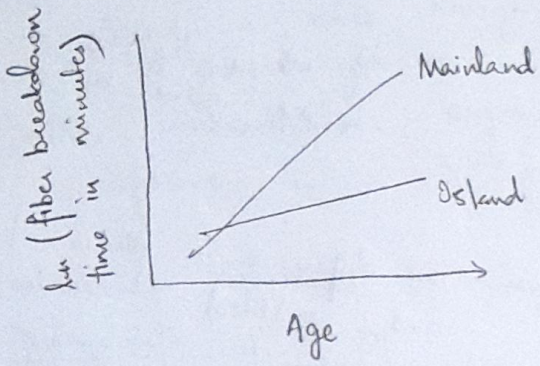
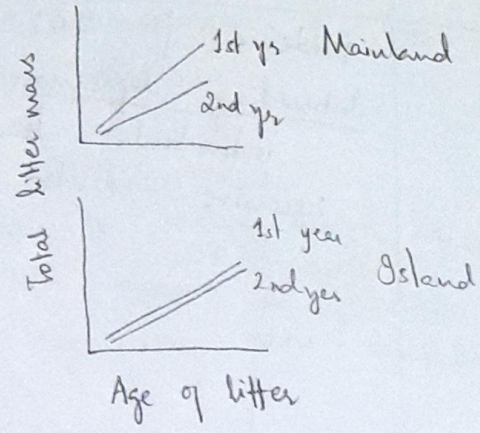
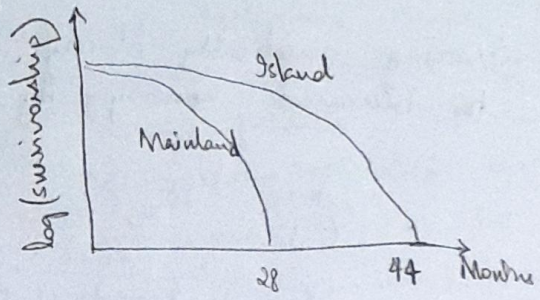
Evidence: Methuselah homozygous mutant

It has greater survivorship than wild type but at the same time, much lower cumulative fertility.

Tradeoff b/w fertility and lifespan.

Opuntias - natural experiment

Mainland & Island populations exist. Much lesser predation risk in island population



longer breaking time  $\Rightarrow$  higher the accumulated metabolic damage

- More aging in the mainland population
- Island populations invest differentially in their first and second litter because the probability of future survival is low in mainland population. This is due to natural selection
- Greater aging & predation decreases the life span.

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Lecture 20

Intraspecific competition

Nature of interaction

Competition	-	-	
Amensalism	-	0	Allopatric chemicals in plants but the secretor benefits or there's too much cost
Predation / Parasitism	+	-	
Mutualism	+	+	
Commensalism	+	0	
Neutralism	0	0	- no interaction

Elephant trampling

hitchhiker fish  
Orchids - epiphytes

cows & egret birds

# Competition

Interaction b/w individuals brought about by a shared resource. This reduces the growth, survival or reproduction of individuals.

Compt. can be interspecific or intraspecific.  
Two types -

## Scramble / Exploitative

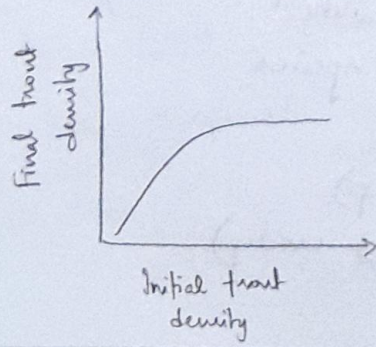
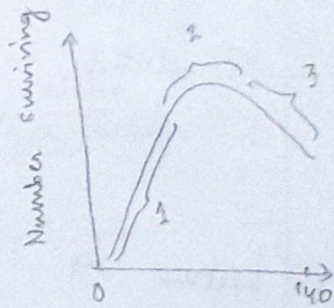
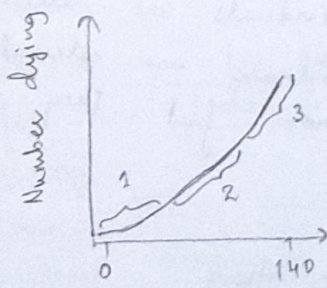
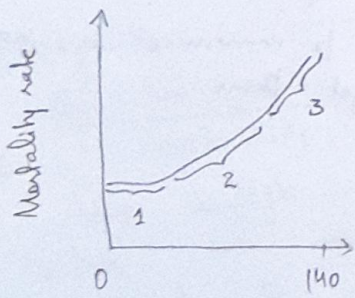
- Resources are shared more or less equally by everyone
- Shortage affects everyone
- Eg: young fish, plants growing in same place

## Contest / Interference

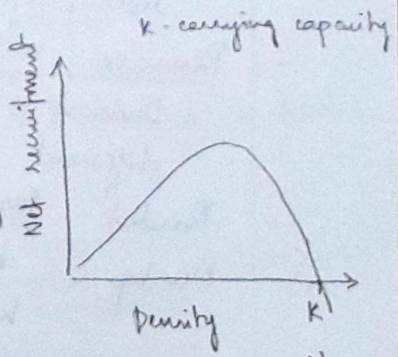
- Resources are shared unequally among individuals
- Winners & losers suffer differently when there's shortage
- Eg: Territorial species

→ Pre-emptive competition  
Based on presence i.e. who came first

→ Density dependent mortality  
Flour beetles - Tribolium confusum



Perfectly compensating density dependence in trout



**Net recruitment** = No. born - No. dying

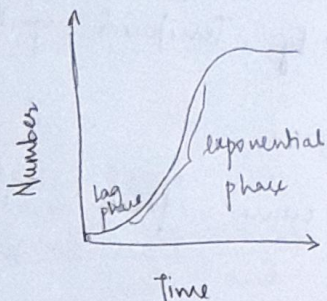
Net recruitment : increases, reaches optimum, then decreases.  
If  $N_t$  is  $-ve \rightarrow$  population is declining  
 $0 \rightarrow$  no growth in population.

Carrying capacity

It's determined by the birth and death rate - when they're equal, the number of  $\beta$  individuals at that state is  $K$ .

Eg: Brown trout - lot of fluctuation in early summer population, but late summer population is const. across years  $\Rightarrow$  reflect  $K$  of that ecosystem

Sigmoidal growth curve

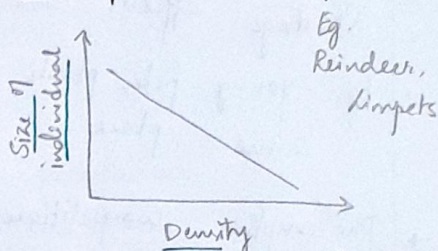


Might not even reach their  $K$ .

$R$  selected - individuals are selected to maximise  $r$

$K$  - selected - individuals are selected to maximise  $K$ , not how fast they get there

Law of constant yields



It's an empirical generalization about the total biomass production. But the biomass (max) can change based on nutrient availability.

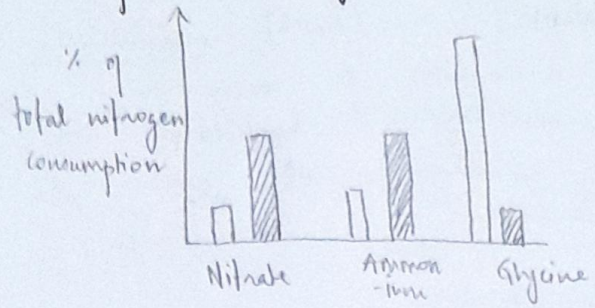
lecture 21

Interspecific competition

- Resource partitioning  
Division & differential utilization of resources by different species in a community.
- Needed for coexistence of the species
- Overlap : diet (resource overlap)  
habitat (physical overlap)  
Time of activity (temporal overlap)

Niche - Fundamental & Realised

Example: Nitrogen niche of *Carex* & *Vaccinium*



Legend:  
 [White box] *Carex*  
 [Hatched box] Nitrate, ammonium

Competing species will try to minimise overlap by maximising partitioning.

Resource overlap  
 High overlap b/w species suggests that population size is kept down by other forces. If species have competed historically, then evolutionary divergence should have occurred.  
 ⇒ Resources are not limiting here - so its potential competition

low overlap suggests that past competition has favored one of the two species  
 Eg: MacArthur's warblers, ghosts of past compt.

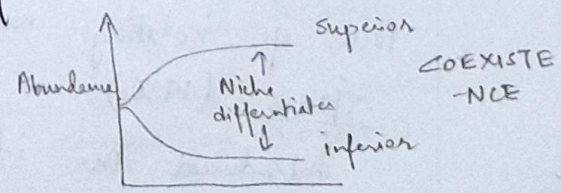
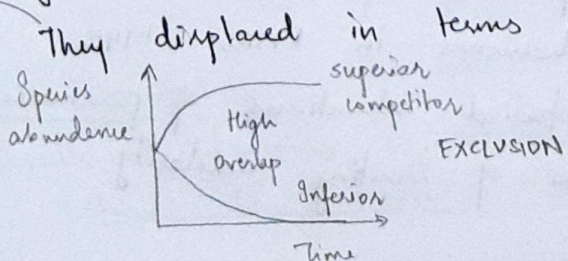
Competitive exclusion

No two species can occupy the same niche in the same community for an indefinite period if they have high overlap.

Neither can achieve their max population density  
 Concept of 'limiting similarity'

One species ends up excluding the other  
 Eg: Anole lizards: Green - native to America  
 Brown - invasive, introduced to Florida

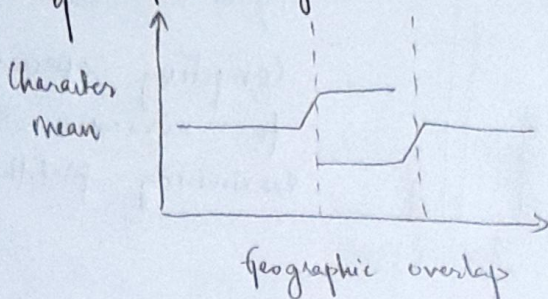
Green anole has been displaced by brown



## Character displacement

Where species overlap, there is a divergence in traits b/w 2 species possibly as a result of competition.

Change in traits (due to overlap) affects the niche of the organism.



Example: Galapagos finches - Grants

Beak size decides the size & type of the seeds that the birds can feed on.

These 3 species - fuliginosa, fortis & maginirostris

- When all species coexist, their character means are different from when they exist alone.

8/11/21

## Lecture 22

## Criteria for character displacement

1. Change in mean value in areas of overlap shouldn't be predictable from variation of overlap
2. Sampling should be done at multiple locations
3. Characters should be heritable
4. Species must be competing for a resource

## History of Competition

- ▶ Lotka & Volterra (early 1900s) - independently arrived at mathematical expressions for resource use
- ▶ Focus of isolating mechanisms in 1930s & 1940s
- ▶ Gauss (1930s) - studied interactions of paramecium  
Introduced the idea of limiting similarity



▶ Importance of ecological compatibility b/w species favoured in 1950s. More interest in mechanism

Hutchinson (1960) - "why are there so many different kinds of animals?"  
This established competition as a major phenomenon in ecology

▶ In 1970s the competition paradigm was questioned & re-evaluated

"Modern" view of competition (Schoener 1982)

1. Species too similar cannot coexist for long.
  - Competitive exclusion
  - limiting similarity - strength of competitive interaction is determined by overlap of characters
2. Species coexisting have sufficient differences in ecological niche as use in resources.
3. Interspecific competition is a strong evolutionary force
4. Geographic distributions of species are often determined by competitive pressures.
5. Species may compete by interference or exploitative mechanism
6. Studies of species with high level of resource overlap should indicate interspecific competition.

Criteria for identifying competition.

1. Competition should explain the distribution & relative abundance of <sup>competing</sup> species
2. Its necessary to show they use common resource which may provide basis of competition
3. There should be evidence that intraspecific competition is occurring based on performance of natural population \*
4. Field manipulations of resources & populations to verify
5. Results of removing or introducing a competing species should be consistent with competition hypothesis

(50)

## Resource overlap studies

8 cyprinid spp. in a Mississippi Stream

Microhabitat distinction by water column position and  
nr of aquatic vegetation were measured for

8 closely related fish.

They found that the niche were quite distinct, with  
some overlap.

## → Warblers feeding zones (ghosts of past competition - MacArthur)

In a pine tree, different species of warblers utilize  
different parts of the tree.

They are partitioned by their microhabitat to reduce comp.

## → Niche segregation of tropical fish community (Silliman 1984)

They considered different features of the stream -

- Slope (steepness & velocity of stream)
- Position in water column
- Food resources.

## → Interspecific exploitative competition - Snail & Caddis fly larvae

- Compete for periphyton

- 6 streams with snail and 6 without

- In streams without snails, the size of caddis larvae is  
~ 2x larger & there's more periphyton in the stream

## → Interference competition - larvae of midge & black flies compete for space on stone surface

- Strong inverse relationship between species densities

- Black flies 'nipped' at midges in reach & disrupted feeding

- Midges were significantly larger when reared without  
black flies.

Lecture 23  
Logistic growth model

Sigmoidal wave

$$\frac{dN}{dt} = rN \left[ 1 - \frac{N}{K} \right]$$

K: carrying capacity  
Growth rate decreases as  $N \rightarrow K$   
r: intrinsic growth rate

Lotka-Volterra Summary

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

$\alpha_{12}$ : competition coefficient  
Translates individuals of sp. 2 into sp. 1

$\alpha_{ij} N_j$ : how much does sp. j utilize the carrying capacity of sp. i.

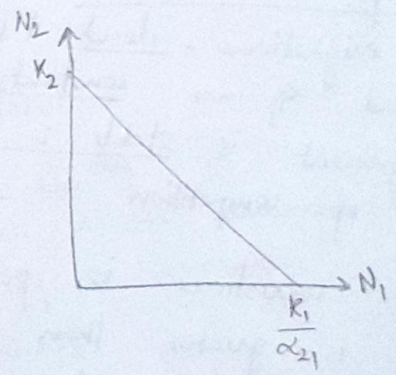
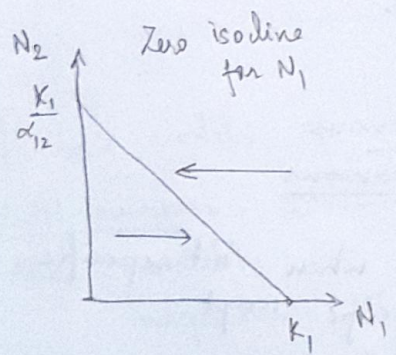
If  $\alpha_{ij} = \alpha_{ji} = 1 \Rightarrow i$  &  $j$  are equivalent competitors

$\alpha_{ij} < 1 \Rightarrow$  effect of  $j$  on  $i$  is less than 1  
interspecific < intraspecific compt.

$\alpha_{ij} > 1 \Rightarrow$  intra < inter

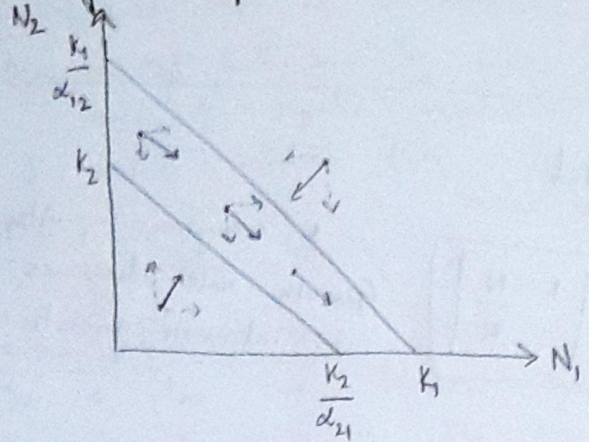
Zero growth isoclines

When  $\frac{dN}{dt} = 0$ , there's no growth. We find  $N$  when  $\frac{dN}{dt} = 0$



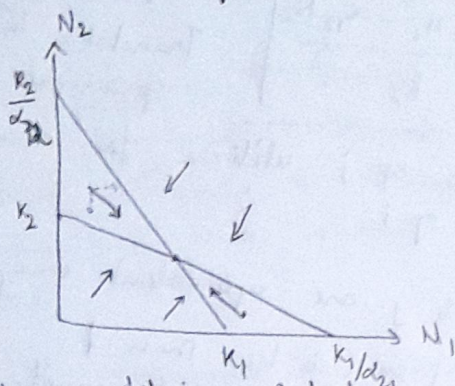
Isocline for sp. 1 represents a combination of abundances of 2 species where sp. 1 population doesn't increase or decrease  
Steeper slope  $\Rightarrow \alpha_{12}$  decreases  $\Rightarrow$  effect of 2 on 1 decreases  
(for  $N_1$  isocline)

### Arrangement of 2 isolines.

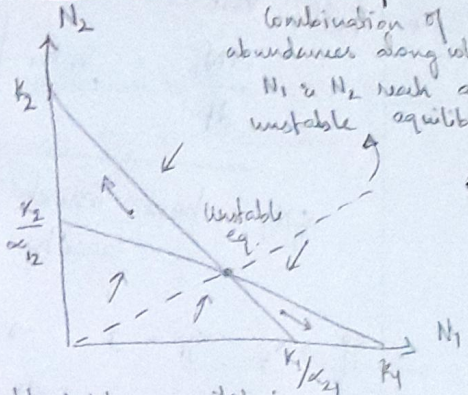


If we're into the region or any region between the two isolines, then we'll always go to  $K_1$ , so that  $N_2$  gets competitively excluded. This is a stable equilibrium.

The result depends on  $K_1$  &  $K_2$  & values of slope



Stable equilibrium, initial conditions don't matter. Both species reach zero isoline and coexist.



Unstable equilibrium. Initial abundances matter in determining the outcome. Species can coexist, but if perturbed, then one sp. goes to extinction. Combination of abundances along which  $N_1$  &  $N_2$  reach an unstable equilib.

### Assumptions of LV model

- No migrations, closed populations
- $K$  and  $\alpha_{ij}$  are constants
- Environment is stable & homogenous
- Effects of competition are instantaneous

Stable coexistence is possible when intraspecific comp is greater than interspecific comp.

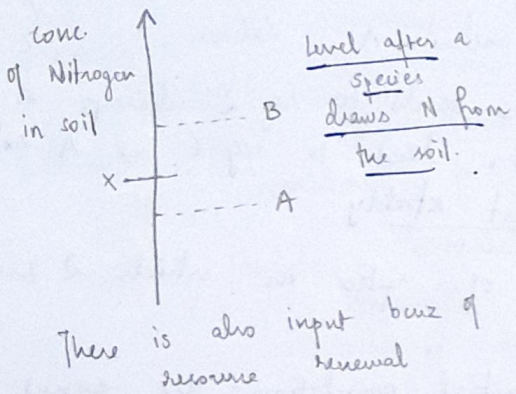
↳ confirm & verify!

### Mechanistic models of competitions

- Incorporates resources through rates of utilization
- $R$  and  $\alpha$  are represented and renewal of resources
- Conditions for coexistence?

### The $R^*$ rule

- The conc. of a resource when a population of a single species grown alone reaches eq. density -  $R^*$
- The winner is determined by which species produces lower value of  $R^*$  in absence of another
- Who can maintain population at lowest level of limiting resources.



At level  $x$ , B cannot survive/grow in the environment (as a population) whereas A population can.

Since A has lower  $R^*$  value, it wins this competition.

### Tilman's models of competition

- Multi-consumer, multi-resource model
- Avg mortality rate of each species assumed to be independent of density & resources
- Supply rates of limiting nutrients
- Population growth rate, assumed to level off due to saturation
- Competition occurs through the effect of each species on the consumed resource i.e. exploitative

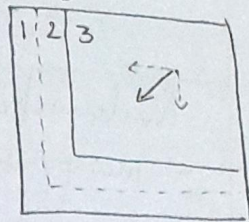
# Lecture 24

## Zero isolines for growth

- Region 1 - below min. conc. for both A & B supply rate  $\gamma$   
 $\Rightarrow$  neither A nor B population will survive

- Region 2 & 3 - Species A\* wins because it has lower  $R^*$

Supply rate  $X$

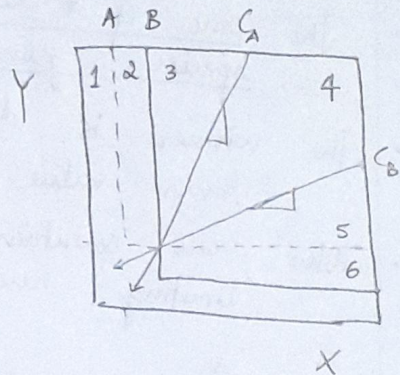


## Graph for competitive exclusion

### Crossing zero growth isolines.

A consumes Y faster/more than X  
 So Y is limiting for A

B consumes X faster, because X is limiting for it



Region 1: neither would survive

2: A competitively excludes B

6: B competitively excludes A

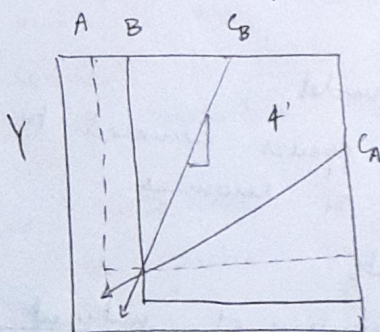
3: consumption vector leads to reg. 2 always  $\Rightarrow$  B extinct.

5: consumption vector leads to reg 6  $\Rightarrow$  A extinct

4: both can coexist stably

$C_A C_B$  - consumption vectors of ratio in which 2 resources are consumed.

This assumes that the initial populations are equal.



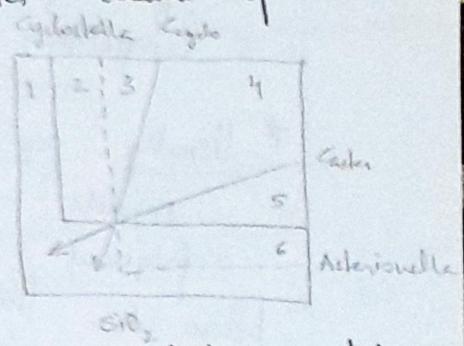
	Limiting	Uses faster
A	Y	X
B	X	Y

Unstable coexistence - 4'

In nature, organisms would be (partly) selected to use the limiting resource faster - more efficiently.  
 So in general, we'll get stable coexistence?

Tilman's experiments - 2 diatom species

- Two resources - phosphorus & silica. Phosphorus is the main limiting nutrient in water because of low solubility of phosphates
- Phosphate limits Cyclotella most
- Asterionella is limited by silica  $P_i$
- $R^*$  values for each were calculated empirically - with expts
- The outcome of competition follows the predicted model
  - 1: both go extinct
  - 2, 3: Cyclotella wins
  - 4: stable coexistence
  - 5, 6: Asterionella wins



Neighborhood models of competition

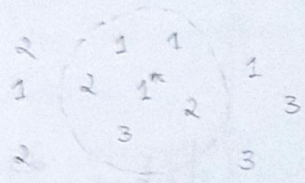
- Previous model worked for phytoplankton where resources are more homogenous
- Doesn't work for land plants where spatial relationships are important to competitive outcome in plants.
- 2 types of models:
  - simulations that keep track of plants spatially
  - analytic model that captures the essence of spatially constrained competition

Neighborhood models

Plants compete within neighborhoods

Final plant responds to competitors within an area.

So, competition with other individuals can be a function of distance

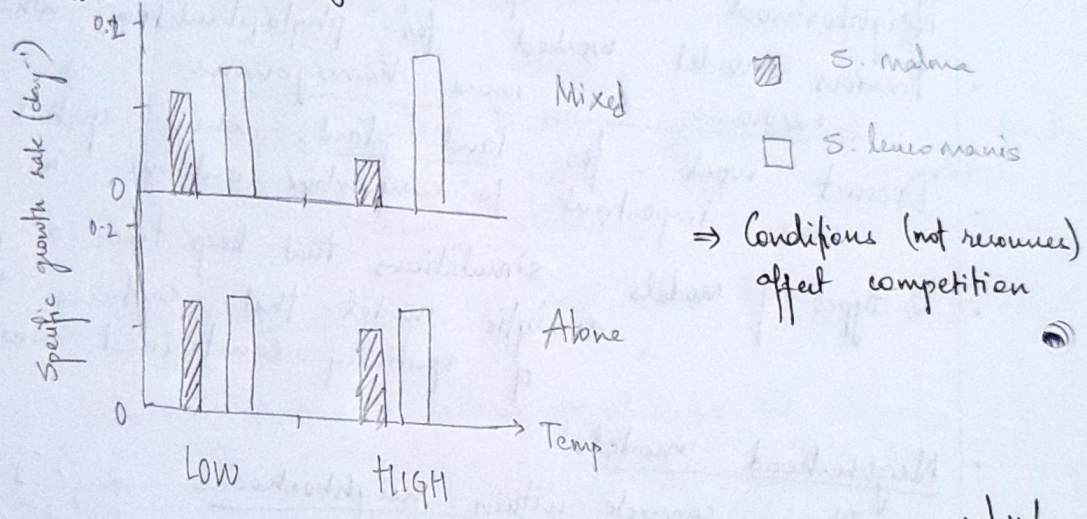


### Assumptions of competitive models

1. Isolated populations
2. Stable & homogenous environment
3. Individuals are homogeneously distributed
4. Effects of comp. are instantaneous
5. Competition is the major/primary interaction affecting populations

# Usually, pop. size is considered close to  $K$  in these models. But high predation/disease rates and frequent environmental changes keeps the populations below  $K$ . This reduces the effects of competition. In this scenario, they're  $R$ -selected.

Competitive interactions are affected by the environment  
 Eg. Salmonid fish grown together or alone at low & high temperatures.



15/11/24

### Lecture 25

Competition for one resource can affect comp. for other resources  
 Eg: Root & shoot competition in corn & pea plants

	Control/grown alone	Root compt.	Shoot compt.	Root & shoot compt.
Biomass of pea plant	100%	57%	90%	53%

# Below & above ground compt. is not necessarily additive



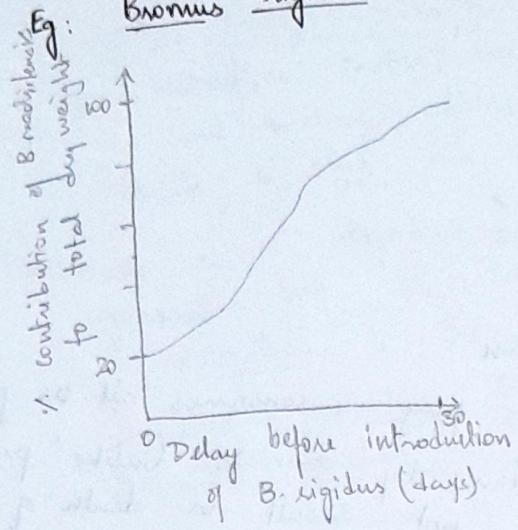
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Pre-emptive competition

Here, the timing of interaction i.e. when the plants are in the environment matters.

It's important for annual plants - when they germinate

Eg: Bromus rigidus vs Bromus medietensis



Delay in introduction of B. rigidus reduces its competitive ability

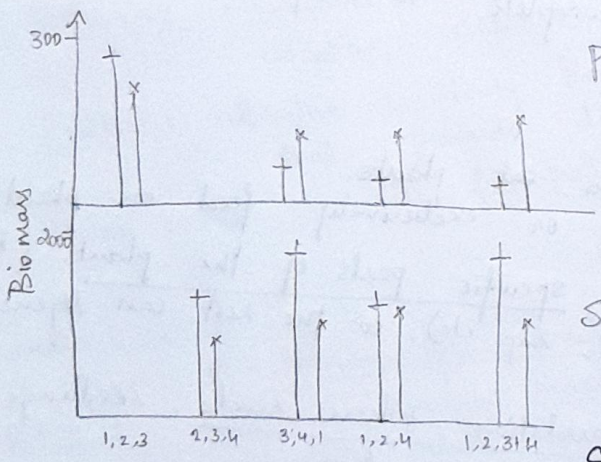
If both start out at the same time, rigidus dominates the interaction

→

Aggregation affects competition (4)

Different species of grasses were grown randomly and in an aggregated manner (where similar species are closer together)

Poa annua (1), Stellaria media (2)



↑ Random ↑ Aggregated

P.a. Aggregated reward is a proxy for intraspecific competition.

⇒ P.a. : interspecific interaction is dominant

S.m. : intraspecific compt. is dominant.

S.m. is a major species competitor, so intraspecific is also high

Mixtures

Indirect or apparent competition

Apparent compt.

Interference

Exploitative

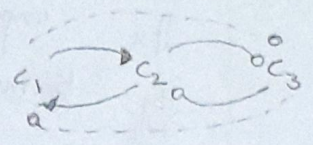
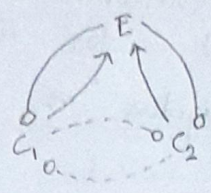
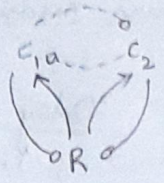
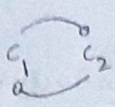
Indirect interaction via shared enemy

Indirect interaction via other species on same trophic level

Natural enemies (E)

Consumers (C)

Limiting resources (R)



— direct      - - - indirect      → +ve      - - - -ve

Major types of consumption

1. Predation: Predator kills prey & consumes all or part of prey
2. Herbivory: Eating of plants by animals. Unlike predation, this may not result in death of plants.
3. Cannibalism: Intraspecific predation - eater & eaten belong to same species
4. Parasitism: host provides some resource/nutrition to parasites at a cost. host may or maynot die
5. Parasitoidism: larvae of parasitoids consume the host to complete its life cycle.

Herbivory

- Occurs when animals eat plants.
- Herbivores primarily or exclusively feed on plants
- Generally restricted to specific parts of the plant (leaves, flowers, roots, sap etc), so the rest can regenerate
- Herbivory resembles predation when seeds, seedlings or whole plant is consumed

- Vertebrate herbivores - wild buffalo, rhinoceros, Indian bison
  - Grazers - grasses & forbs
  - Browsers - tree leaves

- Invertebrate herbivores
  - Half of insect species are herbivores
  - Eg: butterflies, moths, weevils, leaf beetles, gall wasps, leaf mining flies, plant bugs, mites, millipedes
  - Snails & slugs are also largely herbivores.

- Herbivory is a negative interaction for the plant, in general but it can have positive impacts on the ecosystem & the plant -

1. Increased production & nutrient uptake
2. Increased quality of leaf litter & soil - nutrient recycling
3. Increased chances of successful seedling establishment
4. Improved conditions for plant growth (pruning effect)

- Evolutionary responses to herbivory
  - Mechanical protection: thorns, hooks, spines, microscopic crystals in tissues
  - Defensive chemicals: strychnine, morphine, caffeine, nicotine, digitoxin etc.
  - Fruits: attractive & tasty tissues surrounding seeds that promote dispersal
  - Nectar: as reward for pollination.

\* Cannibalism  
 A form of intraspecific predation  
 \* Relatively common among insects when density is high  
 \* Usually involves adults consuming eggs & larvae  
 \* Demonstrated to be a density-dependent factor regulating experimental insect populations

60

## Parasitism

- \* One individual of a species consumes issues or nutrients of another species (host).
- \* Parasites - live in/on their host, often for long are mostly smaller than host are not necessarily fatal to the host.
- \* Examples:
  - Invertebrate parasites: Tapeworm (intestinal parasite of vertebrates), Deer tick, wood tick (external → →)

Vertebrate parasite: Lamprey (jawless fish) - introduced to Great Lakes of N.A., led to decline of whitefish & lake trout

## Parasitoidism

- Insects (flies & wasps) lay their eggs on living hosts. larvae feed ~~on~~ within the body of the host, causing death
- Parasitoids locate their host by responding to airborne chemical signals
- Initially thought to be less important. We now know that >10% of all species are parasitoids
- Eg: Tachinid fly lays eggs on hornworm (moth larva)
- Ichneumon wasps
- Tse-tse fly: humans - sleeping sickness

10/12

Lecture 27 - 17/11

## Herbivory

Consumption of all/part of the plant -

- folivore: leaf predator
- granivore - seeds
- frugivores - fruits
- grazers - eat grasses
- browsers - eat shrubs & trees.

How much do herbivores eat? Young leaves are preferred over old

- ~ 10% of leaves of forest trees
- Tundra - 3%
- Forests: 4-10%
- Grasslands: 10-15%
- Rangeland/grazing system: 30-60%

Bottom up limiting resources - water, nutrients, light  
Top down - herbivory (but its only 10%) - So how important is this factor?

So, primary producers are not strongly regulated by top down forces, rather by bottom up - so competition is very high.

What does 10% mean for herbivores - it means bottom-up regulation is weak, so they are controlled by predation & other top-down forces.

"World is green" - Hairston, Smith & Slobodkin (HSS)

Producers are limited by resources  
Herbivores are limited by predators, not plants  
Predators are limited by prey availability

But such trophic cascade models are too simplistic. Herbivory has had dramatic effects -

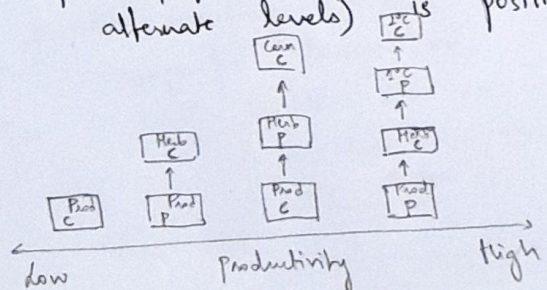
- \* {
  - evolution of defensive compounds
  - community composition
  - reduce productivity
  - affects seedling survival and demography
  - seed predation.

Arguments against HSS theory

- Not all plants are equally green - nutritionally quality varies & some have anti-herbivory compounds
- Herbivore populations nesting sites, territory availability maybe limited by other factors -
- Most food webs are much more complex, more reticulate. Removing one component can affect everything else.

Fretwell's theory (1977)

The trophic complexity (alternate levels) is



(regulation by competition & predation is positively correlated with productivity) Greater the productivity, greater the no. of trophic levels. If there are odd no. of trophic levels, then producers are regulated by competition.

Herbivory has negative effects not just mortality -

- Reduced seed set / fruit abortion
- Reduced size / growth rate
- Change in architecture
- Delay / prevention of maturity

All this affects plant fitness.

Grazer density effects

- \* High densities of herbivores - reduced plant diversity where community is dominated by grazer-resistant species
- \* Moderate density - positive impacts, mutualistic relationships

McNoughton (1979) - regularly grazed plants have higher productivity & attractive to other species of grazers. Leads to coevolution of plants & their herbivores (eg. buffalo saliva & urine).

When part of plant is taken away, it alleviates some nutrient limitations for the plant - which increases productivity in terms of biomass.

Overgrazing

Increase in livestock since 1950 has led to severe overgrazing. The result is deforestation, degradation, deterioration of grasslands, desertification. Encroachment, burning, logging etc

Plant defenses - mechanical (thorns, spines)  
chemical

When F+, effect of spiders is apparent.  
 When F-, presence or absence of S doesn't matter much

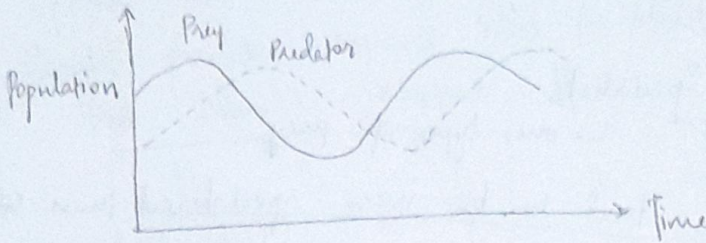
Lecture 28

Predation

Conspicuous interaction - one individual kill and consume another species

Most thoroughly studied consumptive relationship of high ecological and evolutionary relevance

Results - predators has little/no effect on prey population  
 predator eradicates prey population & goes extinct as a result  
 predators & prey coexist dynamically



There are yclical patterns of predator & prey population numbers. There's a phase shift because there's a lag for reaction/response time of predator nos. based on prey nos.  
 Eg: Snowshoe hare & Lynx

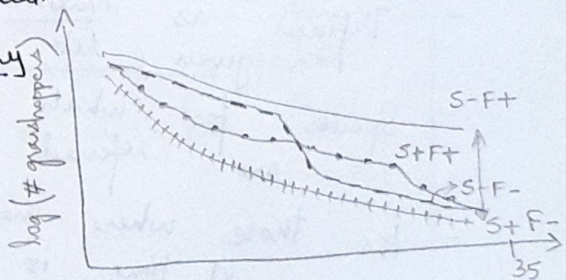
Effects of predators on prey

Most direct effect - reducing number of prey  
 But we assume that predation is random. if weaker individuals are picked off, then they're demographically less important. => predation might not have that big a negative effect on the population

Also, there might be compensatory growth resulting from reduced intraspecific competition

When F+ : S- is better than S+  
 F- : S- is somewhat better than S+ but not ultimately

S-F : shows that S is required for population control.



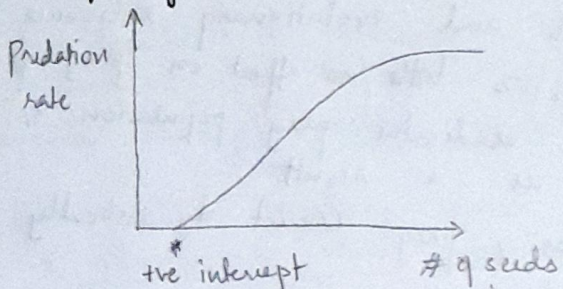
Time (days)

S: spiders (predators) F: fertilizers

Conrad diagrams  
 ?

### Effect on consumers/predators

Increased predation should lead to an increase in predators  
 But - consumption has to exceed a threshold for maintenance  
 consumers maybe satiated. Eg: masting - synchronous  
 flowering floods an area with resources, s.t.  
 predators are satiated & enough prey survive  
 quality and quantity matter.



∴ we need a threshold of prey to maintain predators.

### Generalists and Specialists

↳ several prey sp.      ↳ one type of prey

Usually herbivores tend to be more specialised than carnivores

- Monophagous - exactly one prey Eg: koala, panda
- Oligophagous - few prey types
- Polyphagous - range of plant & animal sp.

### Parasites - generally specialists

Eg Aphids : 80% of 55 UK spp. parasitize on 1 genus

Larger carnivores and herbivores have more varied diet

### Optimal foraging theory

- Relates behaviours of a predator to some "optimal" predicted pattern
- Defined as maximum possible energy return under a given set of foraging conditions.
- Species for which obtaining max amt. of energy is crucial are referred to as energy maximisers
- for those where maximizing food in a given amount of time is vital - time maximisers

What is difference?



Trade-offs shape decisions

MacArthur & Pianka (1966) - model to explain when predators should be specialist or generalist.

Specialists - go for high energy prey  
May spend a lot of time/energy searching

Generalists - spend less energy looking for food  
plenty to pick from, but <sup>not</sup> all of equal or high energy value

### Optimal diet

Should predators expand diet to include other prey?

Diet should expand if -

$$\frac{E_i}{(s_i + h_i)} \geq \frac{E}{(s + h)}$$

E: avg energy content of prey in diet

h: avg handling time (energy) req. to capture, subdue, consume each item

s: avg. search time (energy)

New items will be added to the diet as long as it increases avg energy input.

22/11

## Lecture 29

### Community Ecology

Community: Assemblage of plant and animal populations that live in a particular area or habitat

Populations of various species interact and form this system, with its own emergent properties

Community - biotic component of ecosystem

This field seeks to understand -

- \* underlying mechanisms that create, maintain and determine the fate of biological communities
- \* properties of communities and the consequences of variation in these

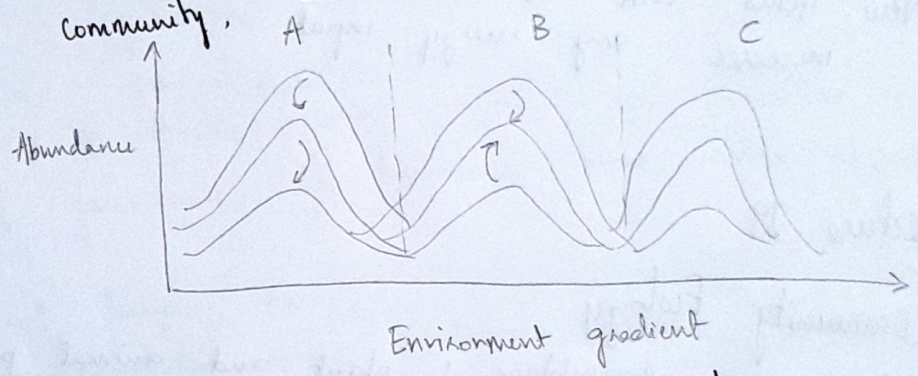
Both have their roots in 19th cent. natural history.

Community function  
 More than the sum of its parts. Emergent properties -

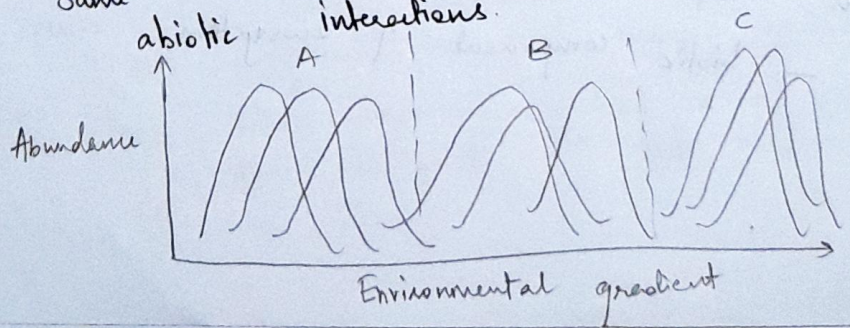
Community productivity      Resilience  
 Community stability        Succession

Two Views of Communities (1900-1950)

→ Clements: interactive concept  
 Considered biotic interactions to be most important in forming a community. These mandatory biotic interactions give rise to an integrated idea of community, as a super-organism.



→ Gleasonian community: individualistic concept  
 Communities are chance assemblages of species in the same area because they happen to have similar abiotic interactions.



# Species pools

## Habitat filtering :

- Dispersal constraints : Geographic species pool
- Environmental constraint : Habitat species pool
- Biotic interaction : Ecological species pool

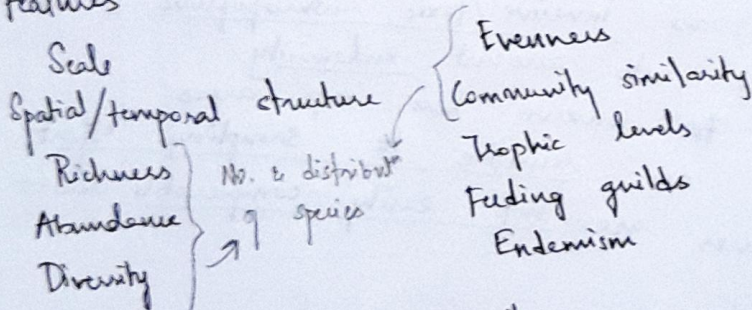
## → Factors influencing structure & composition -

- overall patterns & history/change
- dispersal ability
- abiotic cond<sup>n</sup> & resource availability
- interspecific interaction

→ Competition (bottom up) & predation (top-down) forces are very important in shaping community structure. This sounds mechanistic and deterministic process, but chance plays an important role.

Communities maybe random assemblages - neutral processes.  
 This can be compared to genetic drift in evolution.  
 An extreme view: Neutral theory of ecology

## → Features



→ Scale : size of a community  
can be arbitrary.  
 Provided that the area/habitat's borders are well defined, a community can be of any size

66

## Spatial structure

↳ the way species are distributed in relative to one another. Some species provide a framework that creates habitats for others.

Eg: \* layers of the tropical forest

Emergent canopy → Upper canopy → Lower canopy → Understory → Ground cover.

\* Crest, Slope, Valley

## → Temporal structure

Timing of appearance and activity of species.

Some communities (arctic tundra) have pronounced temporal species. desert plants

## → Richness and Abundance

↳ no. of species

↳ abundance of different species / gross abundance.

These features are commonly used for summarizing. Can be a proxy for diversity, but that can be misleading. Higher richness & abundance doesn't mean its good.

Eg: Panchwati has lesser species than HSER Pune.

24/11/21

## Lecture 30

→ Problem with richness & abundance

Edge species are invasive/toxic, autotrophic & are everywhere

Doesn't take into account endemism

May lead to conserve less imp. areas

The figures are sensitive to sampling effort

These features are not easily comparable across communities

→ Other features

- Diversity

- Evenness

- Trophic levels

- Feeding guilds

- Community Similarities

- Vertical & Horizontal structuring

$$D = 1 - \left( \frac{\sum n(n-1)}{N(N-1)} \right)$$

Diversity indices

- Combination of richness & abundance, combining them in different ways
- Sensitivities: unevenness & low absolute nos. leads to strange results  
unequal collecting/sampling effort

Common indices

- Shannon - based on theoretical basis from signal theory
- Brillouin
- Simpson
- Fisher's alpha - more about abundance, not species no.?

Simpson's diversity index

$$D = 1 - \sum (p_i^2)$$

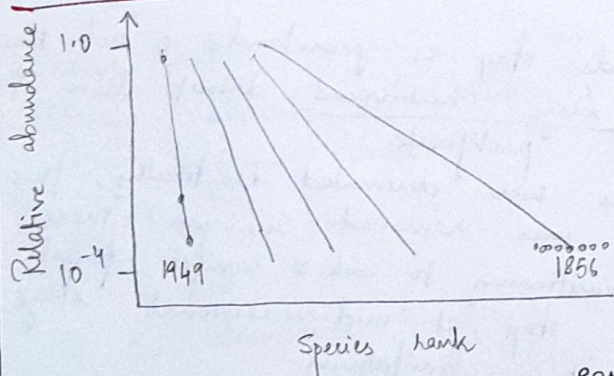
$$p_i = \frac{\# \text{ individuals of } A}{\text{Total no. of individuals}}$$

- With evenness (i.e. equal proportion) of species, D will be maximum. With increasing asymmetry, D will decrease.
- If no. of species increase, the  $p_i$  should increase  $\Rightarrow$  D will decrease.

The index is actually inversely related to the idea of diversity

(?)

Rank-abundance



Increases the asymmetry, sharpens the slope of relative abundance  
More even  $\Rightarrow$  flattens the curve

Rank-abundance curves - easy, graphical way of representing abundance & evenness of species.

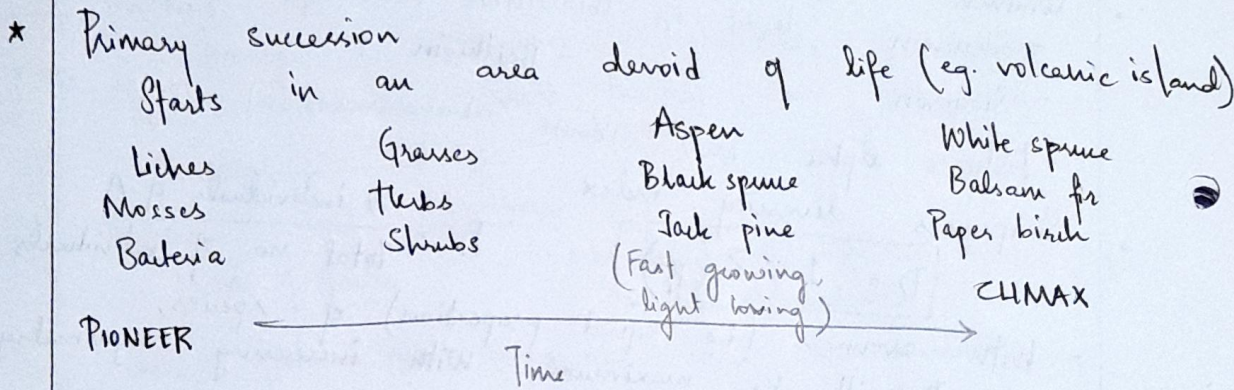
# Succession

In terms of species composition & physical structure, communities change with time

Ecological succession: predictable change in species over time, as each new set of species modifies the environment to enable establishment of other species.

This is virtually ubiquitous.

Early contribution by Clements: analogy of superorganism & developmental trajectories



\* Secondary succession

Occurs due to some perturbation that takes it back to an earlier successional stage (eg. hurricanes, fires)

The final successional state of a system represents a dynamic equilibrium b/w progression & disturbance.

So it might never reach climax community.

10/12

Why do some grasslands stay as grasslands & not become a forest? Large herbivores didn't allow trees and shrubs to proliferate

In NA, when bisons were decimated drastically, this herbivory pressure was removed. So, now these ecosystems are transitioning to oak & conifer forest.

Other times, ecosystems stop at mid-successional stage because of other limitations.

Disturbances  
↳ perturbations (floods, fires, droughts) that damage communities, remove organisms and alter resource availability.

Natural agents - large herbivores, storms, volcanoes, floating log

# Floating log - can damage streams & rivers  
↳ caused by landslide

(69)

Anthropocene - current geological epoch dominated by human activity & its effects.

Primary succession  $\approx$  1000 years - very slow

Secondary succession  $\approx$  100 years - relatively faster

Succession is a ubiquitous phenomenon. The proposed mechanisms are -

1. Competition - colonization tradeoff
2. Niche breadth and similarity
3. Facilitation
4. Interaction w/ enemies
5. Resource ratio hypothesis - differing ratios of resource availability across different stages, and the species that prefer it
6. Vital attributes

→ Competition-Colonization trade-off and successional niche  
Early and late successional species share traits  
that make them good at either col. or compt.  
Late - better at compt.

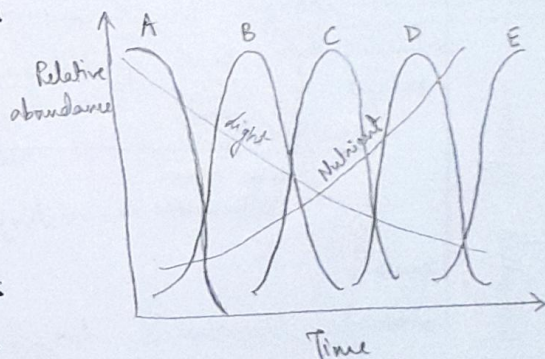
Early - colonization  
Early species persist because -  
• high fecundity & long-term distance seed dispersal.  
• fast growth in nutrient-rich environments ??  
Species can't be good at both. So late species invest more in growth, rather than fecundity

→ Resource-ratio hypothesis - Tilman  
Different nutrients are limiting at different stages

Early  $\uparrow$  light  $\downarrow$  nutrients

Late  $\downarrow$  light  $\uparrow$  nutrients

So the abundance of species is determined by relative competitive ability of plants affected by availability of light: nutrients.



Vital attributes  
 • ability to recover after a disturbance  
 • ability to reproduce in competitive conditions

Facilitation: positive interactions between species  
 ↳ v. important in early stages. Usually early species are nitrogen fixers, allows other species to come in.

Interaction with enemies  
 Herbivores & seed predators can modulate the balance b/w early & late species.  
 Eg: No predators - 3 years to dominate } Golden-rods  
 Predators - 5 years

10/12/2021

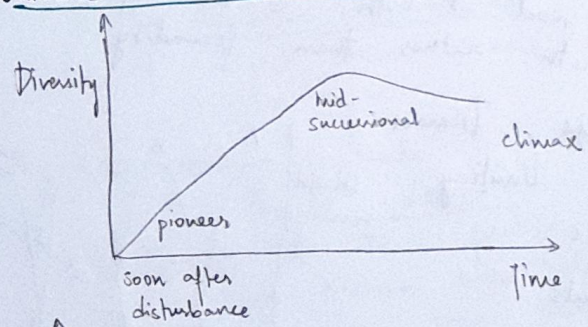
### Lecture 25/11

Patch dynamics: spatiotemporal view of communities

Habitats are patchy in time & space  
 Small scale disturbances (tree fallings) create gaps & patches  
 Disturbed gaps are re-colonized  
 They are important in studying how the community deals with disturbance, how recolonization happens

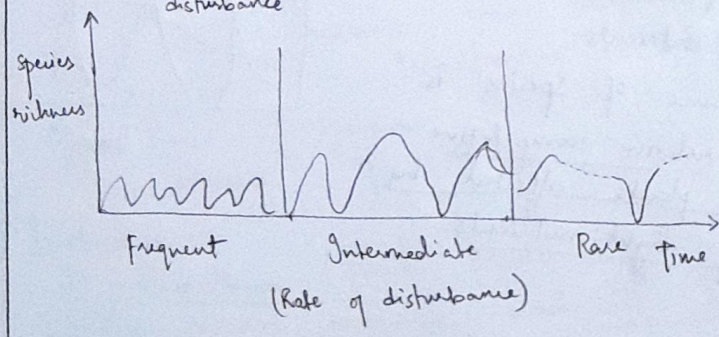
Dominance controlled system - some species are competitively superior  
Founder controlled system - all species have equal competitive ability

### Intermediate Disturbance hypothesis - Connell 1978



After a disturbance, diversity increases to a peak, then decreases slightly because only climax species survive

This is for Dominance controlled systems



Connell - highest diversity at intermediate frequency of disturbance  
 when rare - community dominated by climax species  
 when frequent - community dominated by pioneer species.



### Founder controlled systems

- Equal & random chance of colonization by different species, so after a disturbance, what matters is who gets there first
  - Diversity doesnot change with time since disturbance
  - High levels of diversity can be maintained
- Eg: Great barrier reef

### Energy flow through ecosystems

Ecosystem energetics - Lindermann 1942 - quantified energy transfer b/w trophic levels.

Engene Odum - focused on energy transfer as well as nutrient transfer, so biogeochemicals are important  
Wrote an influential textbook ~ 18:20

### Defining an ecosystem

these too, delineating boundaries can be arbitrary.  
It depends on the scale of questions being asked -  
small scale - soil cores to study microbial interactions  
large scale - grasslands  
Sometimes, there are natural boundaries that delineate ecosystem (eg. lake, agricultural fields)

Energy flow studies assumes that its a closed system in equilibrium  
Early Also that they're self-regulating and deterministic  
stable end points as cycles  
absence of human influence

Contemporary view recognizes non-equilibrium & also -  
 \* new assumptions {
 

- losses & gains
- no stable equilibrium
- dynamics influenced by ext. & internal factors
- disturbance as a natural component
- human activities have a pervasive influence

Ecosystems are v.v. complex, so most researchers specialize in a field

Ecosystem properties -

Productivity

Gross primary productivity (GPP) - energy fixed through photosynthesis total production at primary trophic level

Net primary productivity (NPP) - its GPP minus energy lost by plants through respiration. Biomass accrued is a measure of NPP

Autotrophic respiration  
Ecosystem respiration

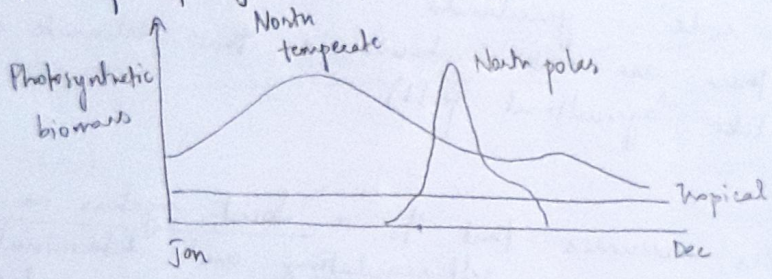
Measuring energy flow

Biomass - measured as dry weight (but amt. of water is variable). Mainly focus on plants (since they're the producers and also biomass at higher levels can be estimated).

Calorimetry - measuring the energy of a sample

Other measures - CO2 uptake (photosynthesis)  
O2 output (respiration)  
Chlorophyll concentration, C-14 ratios, transpiration, remote sensing

# Map of global productivity



Plants make upto ~80% of biomass, energy accumulated in biomass is about 6% of incident solar energy. Herbivores eat only 0.8% (?? 10-15%?), the remaining is decomposed.

Plants use upto 70% of their energy for maintenance. Only 10% of energy is transferred to the next trophic level - ecological efficiency.

The biomass distribution on earth

Plants > Bacteria > Fungi > Archaea > Protists > Animals  
82%      13%      humans: 0.01%

83% wild mammals  
80% avian mammals  
50% plants  
15% fish

Since human civilization, reduced by -

Birds - poultry: 70% wild: 30%

Mammals - livestock: 60% humans: 36% wild animals: 4%

Net primary production in ecosystems

Swamp & marsh > Tropical > Temperate forest > Grassland ... >  
 Aquatic - Tundra > Desert  
 (Temperature) (Water)  
 Algal beds & reefs > estuaries > lakes > Continental shelf > open ocean  
 (Nutrients & light)

Humans use, waste or destroy 27% of total NPP and  
 40% of terrestrial ecosystem  
 Before this expt, most studies were descriptive 11/12

Lecture - 29/11

Cornell 1961

Experimental design - 2 species of barnacles and carnivorous gastropod  
Balanus balanoides (S) - large barnacle, Boreal species  
Chthamalus stellatus (C) - small barnacle, Mediterranean sp  
Thais lapillus (T) - predatory snail  
 ↗ marine, sessile molluscs filter-feeders  
 ↓ more tolerant?

Observation: disjoint vertical distribution of adults of two barnacle sp. in intertidal zone  
 • Adult distribution more restricted than recruit distribution

- Distribution of S & C overlaps significantly as recruits, not as adults
- Thais found only in adult distribution of Balanus

This paper shows how dispersal, abiotic factors, competition and predation affect spatial distribution.

# Tidal levels also vary throughout the year based on gravitational pull exerted by sun & moon

Litoral zone - intertidal zone  
 High tide organisms have to bear desiccation and high T stresses.

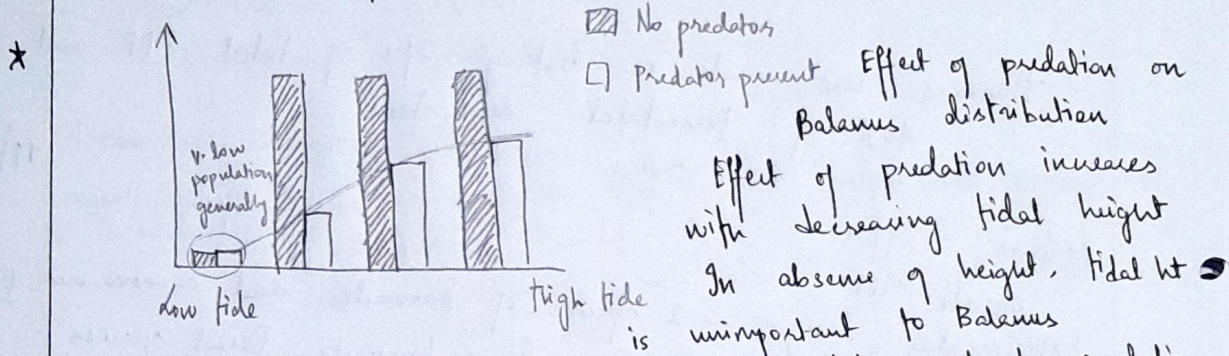
Abundance distribution graphs -

1. Distribution of adults is more restricted than larvae.  
 ⇒ adults are not limited by dispersal ability (upper limit of dist)
2. Chthamalus can be found at a higher tidal level than Balanus because its more resistant to desiccation stress.

74 3. Predation is not very important for dist. of *Chthamalus*, since (this) it's not found there. It's an important factor for *Balanus*.

4. At lower tide levels, *Balanus* is regulated by intraspecific competition. The lower limit of *C* distribution is also shaped by its interspecific competition with *Balanus*.

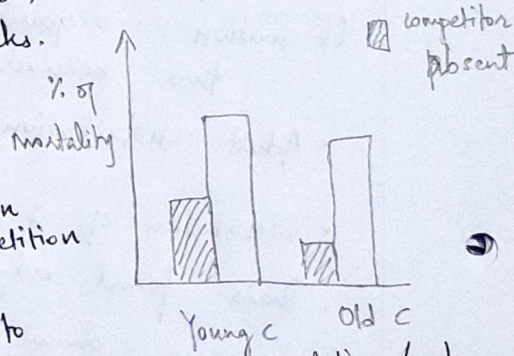
Lower limits of distribution



So lower limit of *Balanus* is determined by predation

\* *Chthamalus* lower limit. He took rocks with *C* from higher tidal zones and moved them to lower levels, and allowed *Balanus* to colonize some of the rocks. He then removed *B* from half of the rock.

*Balanus* limits *Chthamalus* distribution and abundance  $\beta$  through competition



Q. How does this experiment relate to the ideas of niche, environmental filtering & predation/cppt?

Ecosystem ecology

Biodiversity - diversity of living things at ecosystem level

Why study? - to understand underlying processes to understand consequences of diversity - relation b/w biodiversity & ecosystem function (stability, product)

Richness, Abundance, } Diversity indices  
Shannon-Wiener index (info theory)  
Simpson (dominance index).

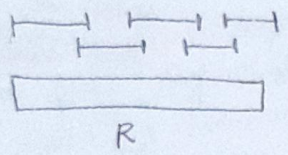
- Two schools of thought on how species coexist -
- Equilibrium theory - ecological & evolutionary compromises lead to resource partitioning
  - Non-equilibrium theory - fluctuating conditions keep dominant species from monopolizing resources

Resource partitioning (Eq. theory)

↳ among spp. in a community increases sp. richness and reduces competition  
 Competing species are more likely to coexist when they use resources in different ways  
 Eg. warblers inhabit different microhabitats in the tree

Species richness model

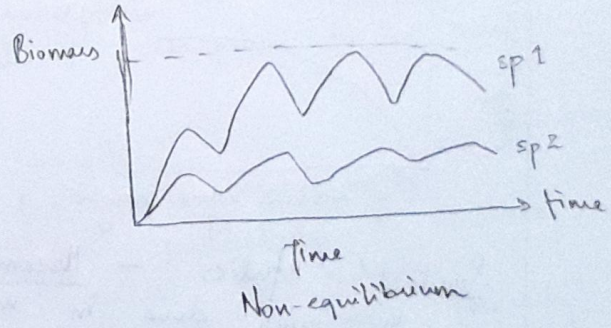
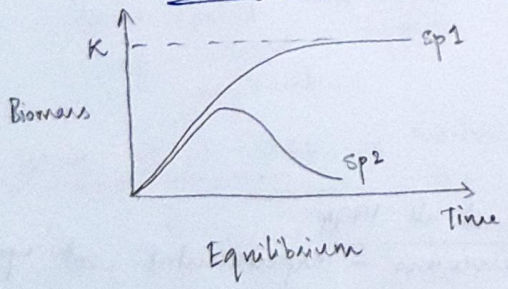
We can increase the number species by -



1. Increasing the available resources.
2. Decreasing the range of resource utilization i.e. narrower niche breadth - overlap decreases
3. Increasing niche overlap. (increased comp.)
4. Fill the open niches, if they're not filled already

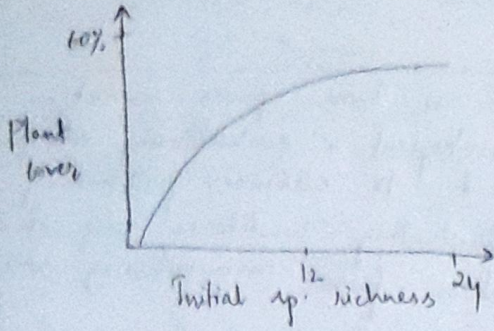
Non-equilibrium theories

Processes such as stress, disturbance or predation can mediate resource availability (prevent comp. exclusion) and encourage coexistence



Non-equilibrium theory - intermediate disturbance hypothesis

Biodiversity is related to ecosystem productivity - Tilman 1996



Increases sharply initially, then plant cover plateaus with further increase in richness

Lecture - 1/12

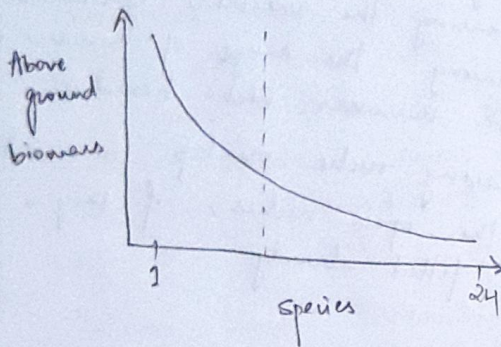
11/12

Experiments show that sp. diversity is positively correlated to ecosystem function and community function like productivity, resistance and resilience

Perhaps this increase is because increased species would be able to utilize nutrients better, more efficiently

Also monocultures are more susceptible to disturbances.

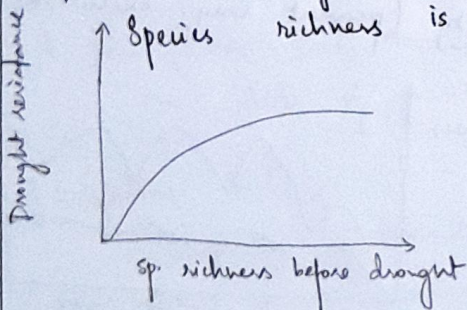
Also - more species - higher chance of mutualistic interaction



Some species contribute more to productivity than others. With increase in sp. no. in treatment, the prob. that the "real prod sp" is included in the treatment increases.

Assignment 2.

Tilman & Downing 1992



Species richness is positively correlated to community stability. Resistance was measured as biomass difference before and after the drought

Seminal studies - Naeem et al 1994

It was done in mesocosms - experimental set up with decomposers, 1° producers, 1° & 2° consumers. They had high, medium and low biodiversity systems

\*  $CO_2$  flux - highest in high diversity \* % change in plant cover increase w/ increase in diversity

lower in low & med diversity

Tilman et al 1996 - loss of biodiversity will affect productivity & sustainability.

Hector et al 1999  
8 different sites - experimental study with different species richness.

In 5 sites, biomass increased with increase in species in 3 of them, there was no correlation.

There have been a lot of experiments since then many found that there's a positive correlation, while almost equal no. of studies found no correlation

Hoopes et al - biodiversity v. important  
Srinastava & Velland - for some ecosystem functions, identifying functionally important species can be more useful

Balmaceda et al 2006 - metaanalysis  
446 measures of biodiversity assess (252 in grassland)

- Clear evidence that biodiversity has positive effects on most ecosystem functions
- Effects on stability measures are not stronger than effects on performance measures
- Effects are weaker if manipulations are less controlled
- Productivity effects decline with increasing no. of trophic links b/w elements manipulated & measured

Invasive effect  
Monocultures are more susceptible to disturbances. So having more species allows ecosystem to be more resilient.

Warm et al 2006 - Marine ecosystem measurements  
They measured the fish catch measurements

They had different measures - productivity, % recovery, average catch etc against sp richness (linearly)  
They increased with increase in richness (linearly)  
Coefficient of variation (inverse of stability) decreases with increase in richness.

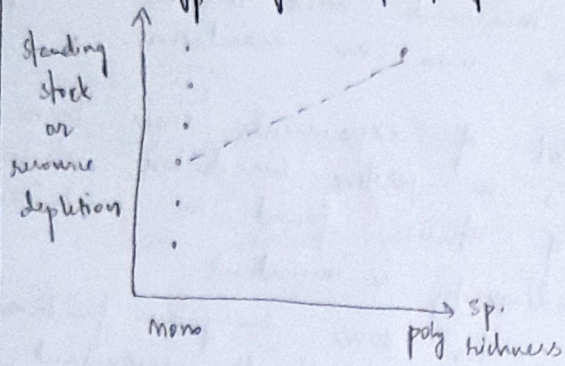
from overfishing

93 studies - 175 experiments

- direct manipulation of  $\geq 3$  species
- 4 trophic groups
- Response variables: standing stock, resource depletion

$LR_{avg}$ : log response ratio on avg <sup>mean</sup>

$y_p$ : yield of polyculture       $y_m$ : yield of most productive monocultures



$$LR_{avg} = \ln \left( \frac{y_p}{y_m} \right)$$

- > 0 : positive slope
- = 0 : flat line
- < 0 : negative slope

$LR_{avg}$  is positive for all trophic levels & aquatic & terrestrial system for standing stock & resource depletion.

So, polycultures are more productive and sustainable/efficient

# Resource depletion is  $\sim 0$  for plants & herbivores - may not have a great effect

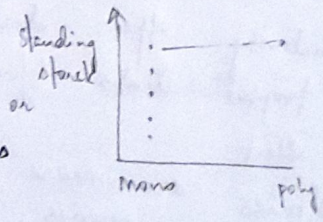
Broadly, we can say biodiversity increases ecosystem function

$LR_{max}$ : max. log response ratio       $y_{max}$ : most productive monoculture yield

$$LR_{max} = \ln \left( \frac{y_p}{y_{max}} \right)$$

Results -

- For standing stock, predators & detritivores -  $LR_{max} < 0$



Resource depletion -  $LR_{max} \sim 0$  for plants

$LR_{max} > 0$  (slightly positive) for others

- For terrestrial & aquatic - large error bars that overlap 0  
So  $LR_{max} \sim 0$ .

This means the effect of biodiversity is not much greater than the most productive monoculture.  
Polyculture is not different than most productive monoculture

Average effect of biodiversity is decreasing biomass



But resilience is an important ecosystem fn that is affected by biodiversity more than most productive sp. There maybe other dimensions to look at, not just productivity.

Food webs are incredibly complex - most productive plant may not sustain the most productive consumers & so on its important to look at system as a whole.

What does this mean for results of Tilman et al 1996? This result maybe a stochastic artefact

What needs to be done?

- 1) Most studies study pattern and attribute a mechanism but only 38% actually test for the mechanism
  - 2) Including multiple trophic levels presence of herbivores affected the LRang values of plants.
  - 3) Moving beyond small scales The mechanisms are happening at a much bigger / longer scale than experimentally tractable scales
- Increasing time scale (ln(generations)) increased LRang & LRmax so there was a (weak) positive correlation b/w biodiversity effects and temporal & spatial scale