

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 [Andrensenha & 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 (ie, 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
- * give 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

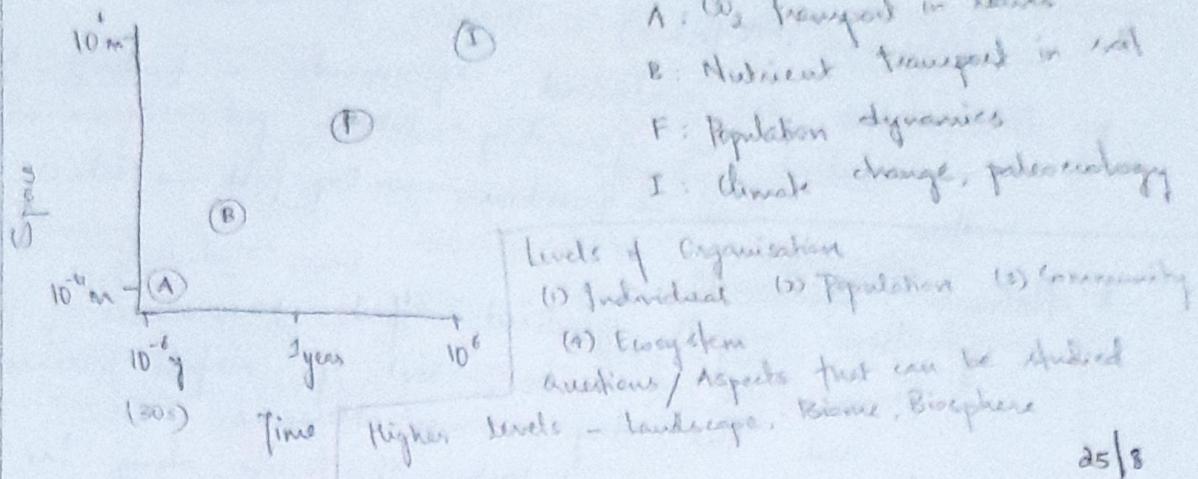
Ecology as a subject overlaps with Environmental Sciences (physical, chemical, E&S aspects), Conservation biology (applied ecology with social components and hugely multidisciplinary) and wildlife biology (emphasis on the wildlife - manage & conserve).

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

Levels of biological organisation

Ecosystem	→ Community	Century	Realm of ecology
Population		Year	
Organism / Individual		Day	
Organ system		Min	
Organ		Seconds	
Tissue		Milliseconds	
Cell		Microseconds	
Subcellular		Nanoseconds	
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



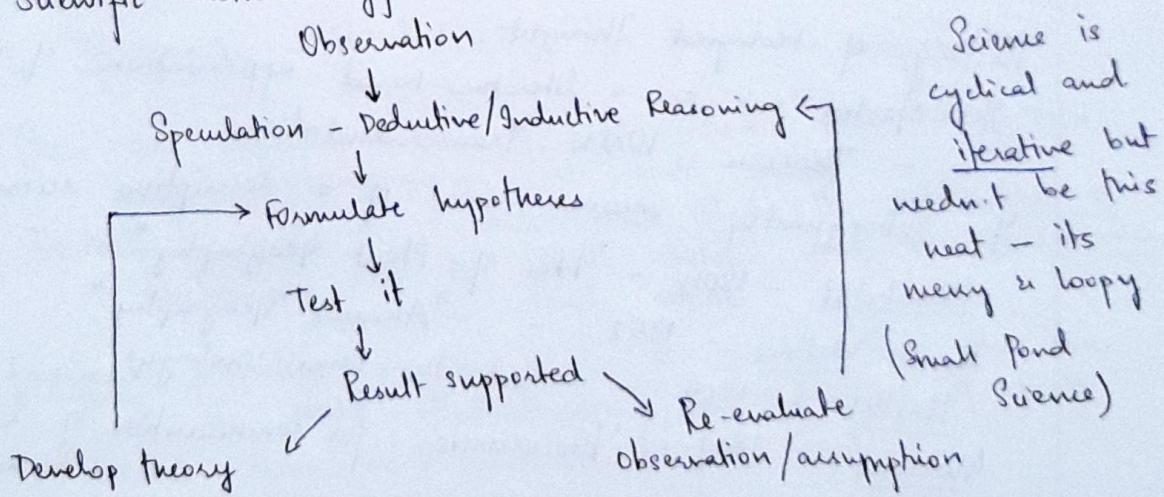
Lecture 04

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

Scientific methodology



④ Experiments

Central component of scientific methodology → treatment group

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

- Fisherian (R.A. Fisher) - analysis of variance

Manipulative or controlled experiments → tradeoff b/w control & generality. Where you experiment matters - Lab → Greenhouse → Exp field → Natural field

Natural experiments

Eg: How rainfall gradient affects performance of plants?
From Pune → Kerala, amount 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 -

Thunboldt - 1804 - "Idea of Plant Geography"

Russell Wallace - 1852 - "Animal Geography"

Haeckel - 1865 - coined the term 'ecology'

Mobius - 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 experiments 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 makes it hard to apply the Scientific method easily

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 phenomena at each level.

Bartolome 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

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
Manímo 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, 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

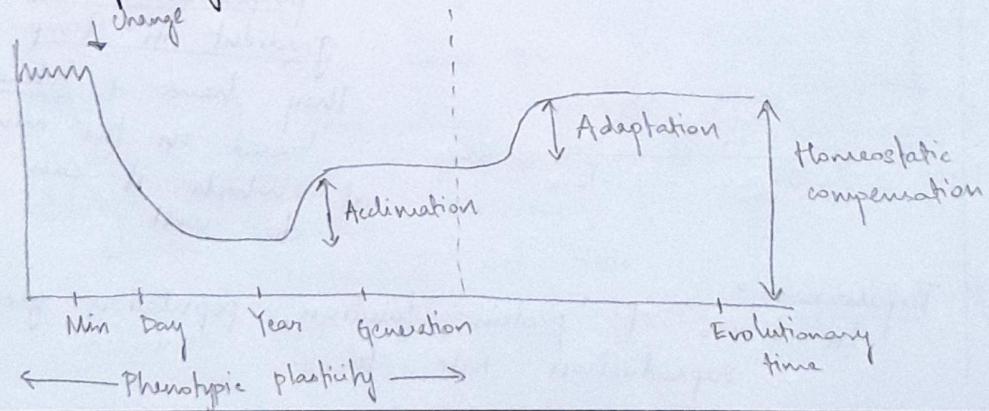
- Differential fitness value / reproductive success

- 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



Lecture 8

Aclimation - 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.

Aclimation - 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 (e.g. 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.

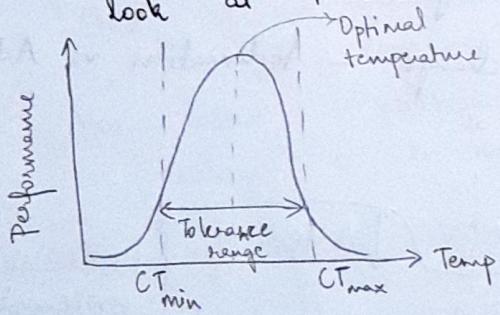
- Abiotic environment can vary on macro & micro scales

- 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

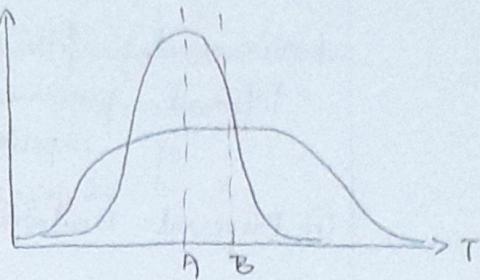


Every organism has a unimodal performance curve for a gradient in temp.

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 breadth.
 - 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 its fundamental limits. It can't 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_2 , T, salinity.

This definition of niche was given by Hutchinson (1958) in a n-dimensional hypersphere 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

* + # △ □ Regional pool
--- ↓ ---

② Habitat filtering

+ # △ Only those whose fundamental niche overlaps with the dispersal range

③ Biotic interactions

+ △ competition, predation etc.
Community

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Lecture 07

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 there effects pervade 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 100 m increase

Proximity to ocean; Aspect - Northern vs Southern slope

Temporal : Season - time of the year

Diurnal - time of the day

Microclimate - 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

Poikilotherm ← Body temp →

Eurytherm (Generalist) ← Niche breadth

Independent of ext. conditions

Narrow but higher p.c.

Expend energy for homeostasis

Endotherms - mammals

Homeotherms

Stenotherm (specialist)

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 too

Example: Skunk cabbage - symplocarpus foetidus.
 This plant just before snowmelt, generates heat through mitochondria as a 2° process of respiration.
 So it develops, grows & blooms early so it doesn't have to compete with other plants.

Temperature & Metabolism [Q10]

within physiologically relevant ranges of T

For every 10° increase in temperature, the metabolic activity of enzyme increases by twofold.
 But this cannot be done indefinitely - protein denature at a particular enzyme

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Temperature and body size

Bergman's Rule

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

This relationship has been shown with other related animals - foxes, rodents
 Pearson: 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 and diversity decreases with decrease in temperature So T also affects higher ecological processes.

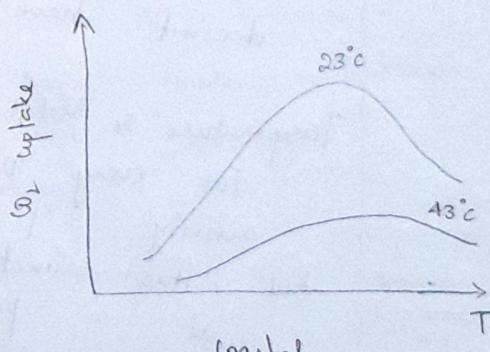
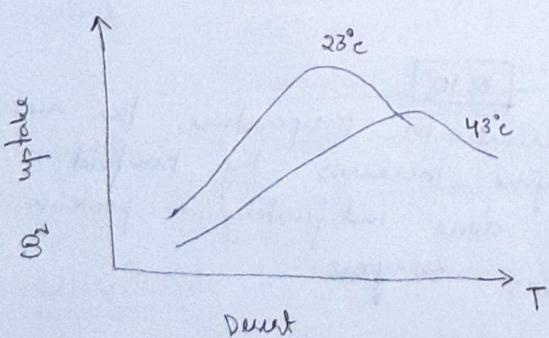
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lecture 08

Acclimation

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

Berry & 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

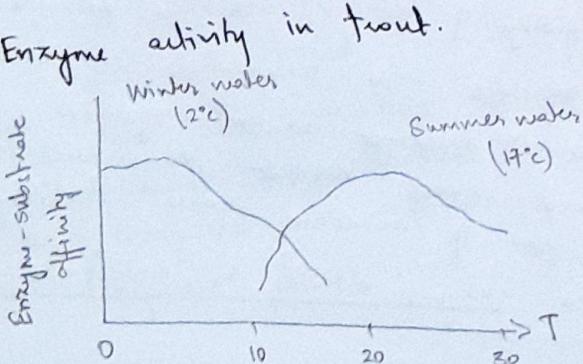
(coastal - specialist (\therefore small range of T). But its performance is not greater than desert plant (generalist). Counter example of VAD)

Need to revisit assumptions

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- * 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.
Max. photosynthetic rate doesn't change - just shifts
- * Coastal plot : The cool-grown plants have similar levels of productivity as desert plants. But hot-grown in terms of performance is higher than cool grown coastal plants. So desert plants have activated without compromising performance. Even the coastal plants have activated, but not very well.
- Possibly \nwarrow : 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.
- Other factors might be important
- So the point is that : the two populations are genetically different \nwarrow they're adapted to their own climates. This means that even adaptability could be different - coastal population can't acclimate to desert conditions anymore

Manning O_2 uptake : A garter 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.

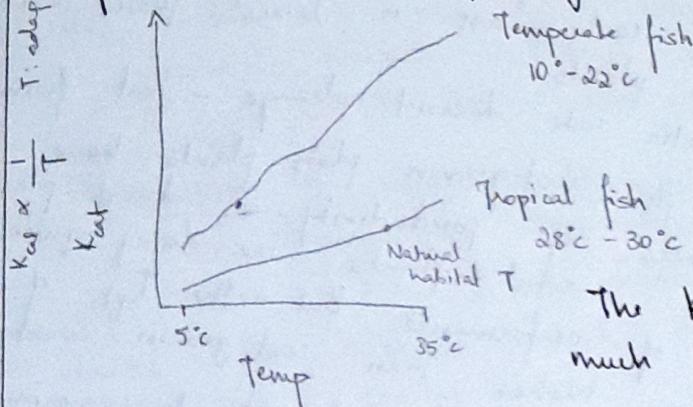
The optimal temp of performance shows a distinct shift.

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

ALSO : K_m of ectotherms is lower than that of mammals.

Temperature adaptation of enzymes - Somero

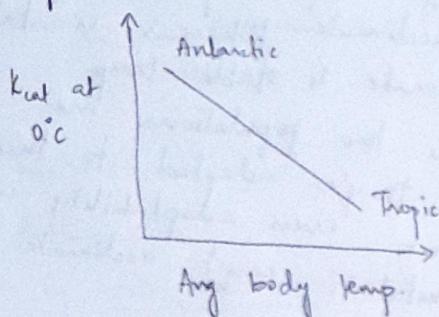


K_{cat} of lactate dehydrogenase. It's the enzyme turnover rate - the amt. of substrate processed per unit enzyme per unit time.

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 less amt of enzyme and save energy?

Ans:

George Somero ~~we~~ notes : $K_m \propto$ 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 ie binding affinity decreases as T increases in an organism.

K_m remains constant across habitat temperatures. ie the enzyme has to maintain some stability. (?)

There's a tradeoff between enzyme activity & substrate binding

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

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).

M.C. 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 & fog

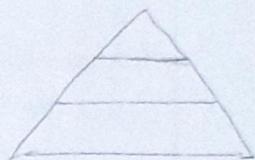
Energy flow in food web.

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 - it's 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

$\frac{1}{3}$ is used up in evaporation & drives water cycle.

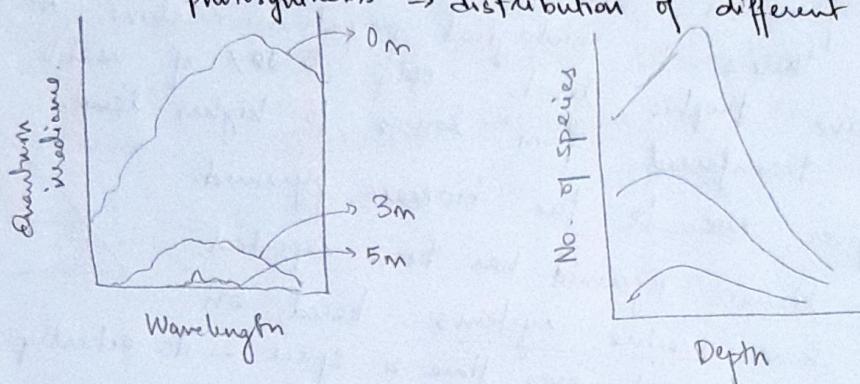
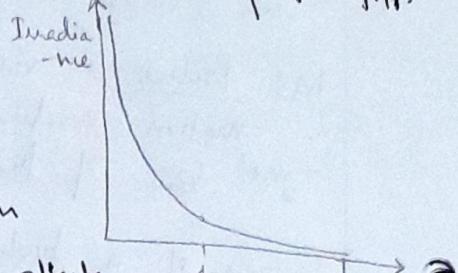
$\frac{1}{4}$ is used up in availability of solar energy.

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

This is also variation at microspatial scales. This is very apparent in tropical forest - the forest floor gets 2x.

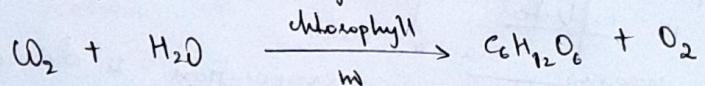
as compared to canopy. It's less prominent in temperate forest and agricultural fields.

- There are also temporal variation in availability of sunlight
- . In tropical region, 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 t 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



CO_2 & O_2 are important for plant metabolism. So they should have an efficient exchange of gases.

In this process, the plants lose ~~to~~ water — 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 hair, 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

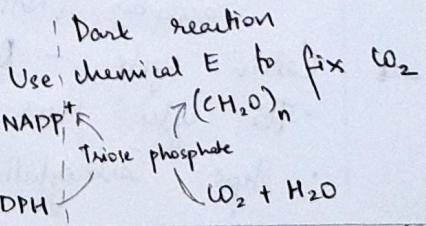
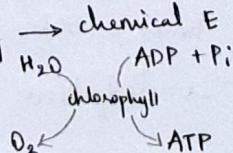
Double-membrane organelle
 Plate-like structures called thylakoid are stacked in structures called grana, which are interconnected by fret lamellae

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.

Light Reaction

Harvest light energy \rightarrow chemical E



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.

→ Photocytotic 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 wavelength
- Chlorophyll has a complex ring structure - porphyrin ring co-coordinated to central Mg atom. The ring contains loosely bound electrons - involved in electron transitions & redox reactions of photosynthesis
- When chlorophyll enters higher energy state, it gives up heat as energy. If it enters lower excited state for few nanoseconds, it becomes unstable and causes chemical rxns to occur
- This energy causes chemical rxns to occur

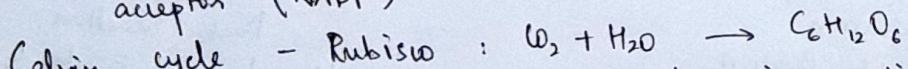
→ Light Reaction

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 oxidatⁿ-reductⁿ rxns where e⁻s are passed from one membrane-bound protein/enzyme to another before finally attached to a terminal electron acceptor ($NADP^+$)



The cycle runs 6 times, each time incorporating a new carbon

Steps: Carboxylation → Reduction → 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 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_i , hypotheses may not be mutually exclusive.

Strong Inference - Platt 1964

Alternate methods - Bayesian methods

} Refer Pignucci

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 vs 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 numbers are influenced by the size of the community - which influences the total no. of publications & total no. of citations.
- * 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 taken cautiously.

We can see the statistical tests used and the
actual scale of studies to augment this word search

Exploring hypotheses refers 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

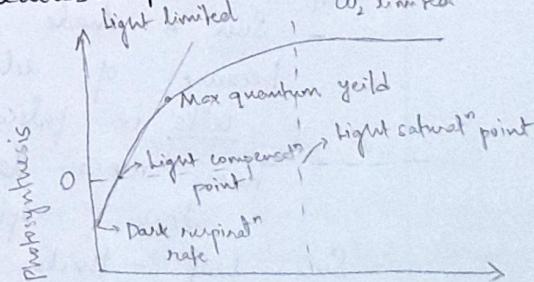
There are different kinds of responses - passive, acclimation & adaptation.

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



Light

Photosynthesis is measured as CO_2 uptake
Photosynthesis increases with light intensity, 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 CO₂

That's why Y-axis (net CO₂ uptake)

is negative \downarrow per unit leaf area
 \downarrow μmoles of CO₂ \Rightarrow per unit time

Light intensity
(Photosynthetically active photon flux density)

Light saturation point

Dark respiration rate

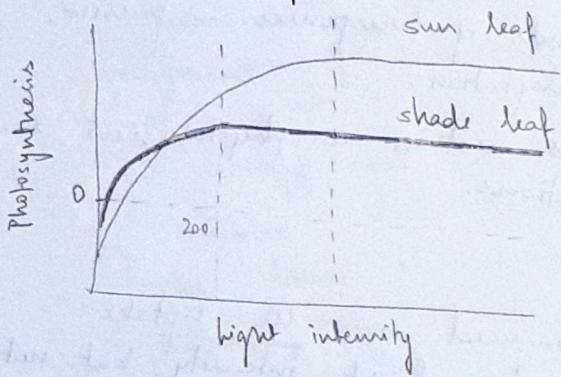
Keeping all else constant: Dark rate, temperature, water availability etc.

Limiting factors: limitations of photosystems in reducing NADP⁺ limitations in rate of reaction → light harvesting
 Increased light ie temp in water-limited situation will make the stomata close, so CO_2 uptake decreases → rate drops.
 CO_2 level at high light intensity is the limiting factor ($\approx 400 \text{ ppm}$)

How will increasing 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
- * Maximum quantum yield: rate of increase of photosynthesis per unit light intensity. (slope of initial curve) (no. of photons)
- * Light compensation pt - light level where CO_2 uptake = CO_2 release
- * Light saturation point - light level where light is no longer limiting by CO_2 photosynthesis. Now it's limited



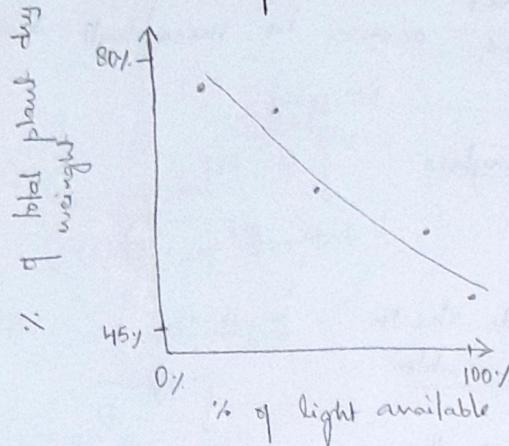
leaves of same plant, acclimated to different levels of light

Shade leaf is more leaf limited by CO_2 after 200 Because of light limitations, if doesn't invest in photosystems that can process higher light levels - so shade leaf becomes 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 leaves ie. palisade parenchyma is densely packed, has more layers. So sun leaf has higher dark respiration rate
 - Sun leaf - thicker leaf with smaller surface area → has more machinery
 - Shade leaf - thinner leaf with larger surface area, to optimise leaves machinery & the chances of catching light

Lecture 12

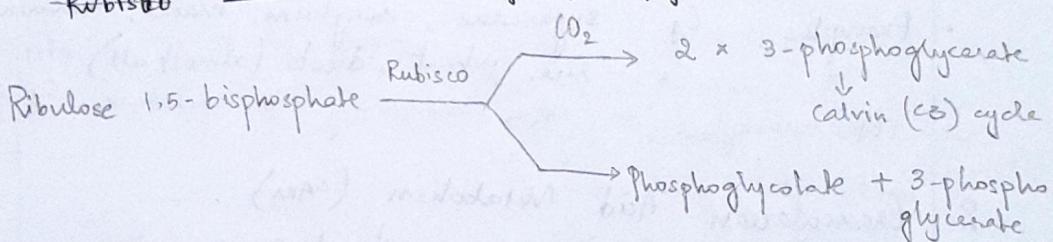
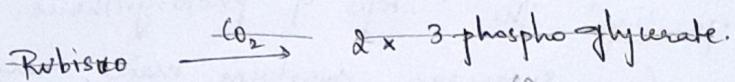
Allocation of biomass to leaves



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. It's used in Calvin cycle
- It catalyses the first step of photosynthesis
- Rubisco reacts with CO_2 , but also O_2 - competing reactions



Rubisco : Competing reactions

It can't discriminate well b/w O_2 and CO_2 . In presence of high O_2 , it catalyses an oxygenation reaction which leads to Photorespiration

Conditions: low CO_2 / high O_2 *
high temperature

Photorespiration is estimated to reduce productivity by 25%

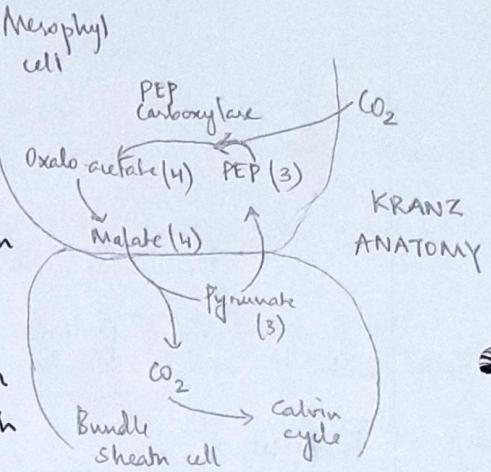
At high T - Ability of Rubisco to discriminate b/w CO_2 & O_2 worsens. Also, when it's hot (& dry), plants close their stomata to conserve water. But they continue to photosynthesize. This creates $\uparrow \text{O}_2$ & $\downarrow \text{CO}_2$ conditions inside the plant

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

1. C₄ pathway (Hatch-Slack pathway)

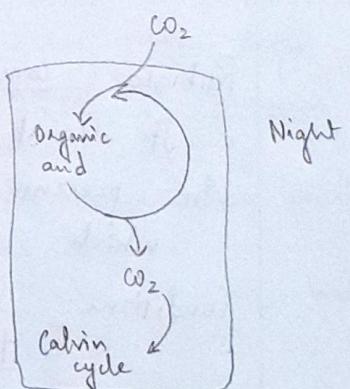
- It has evolved independently multiple times.
- In C₃ plants, all processes occur in mesophyll cells
- In C₄ plants photosynthesis occurs in mesophyll and bundle sheath cells
- An extra enzyme: PEP carboxylase traps O₂ and makes a C₄ intermediate
- This is 'smuggled' into bundle sheath cells which are not permeable to CO₂
- In the BSC, CO₂ is released from 4C intermediate & goes through the usual Calvin cycle.
- This enriches O₂ in BSC & they have less O₂ anyway thus, PEP carboxylase doesn't have an affinity for O₂.
- In this way C₄ plants avoid photorespiration — spatially separating the steps of photosynthesis.
- Examples: C₄: sugarcane, sorghum, maize, amaranthus
C₃: rice, wheat, dicots (almost all)

PEP carboxylase — extra machinery to maintain. C₄ plants pay a cost.



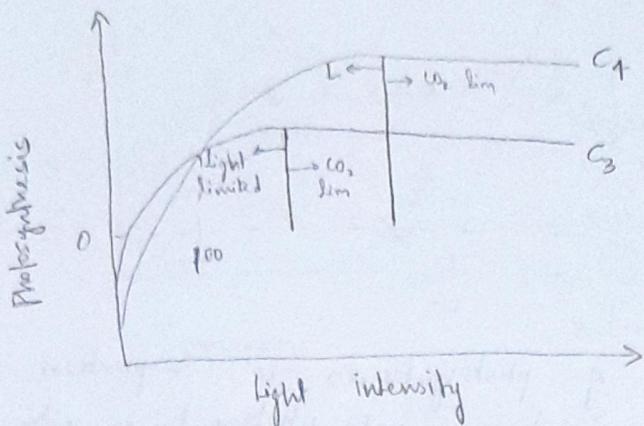
2. Crassulacean Acid Metabolism (CAM)

- O₂ is fixed at night & stored as a 4C organic acid
- During the day, stomata is closed to prevent water loss & stored O₂ is used for photosynthesis
- So O₂ is concentrated during the day and can be used without losing water — if can avoid photorespiration
- This process separates steps temporally instead of spatially
- Eg: succulents, pineapple
- (?) CAM can't avoid photorespiratn entirely — so its less efficient? check.



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

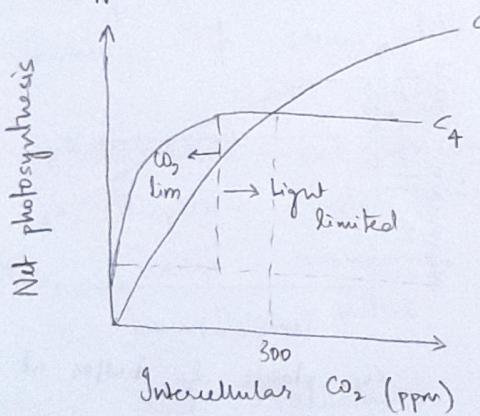
Light response curves ($CO_2 = 350$ ppm)



Discussion:

- C_3 plants are more limited by CO_2 - C_4 plants do okay
↳ too much photorespiratn 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

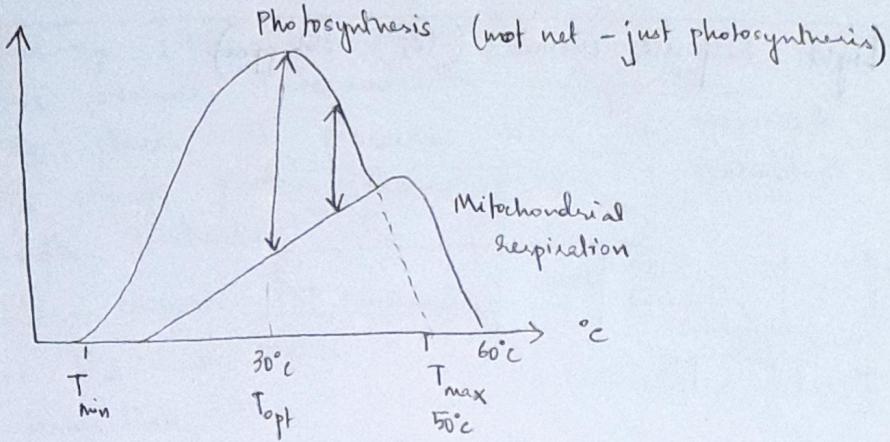


This curve is probably at light intensity < 200 where C_3 is doing better than C_4 with increasing CO_2 .

Changing light levels might shift the curves.

(> 300 ppm)
Very high CO_2 levels - C_3 plants have an advantage

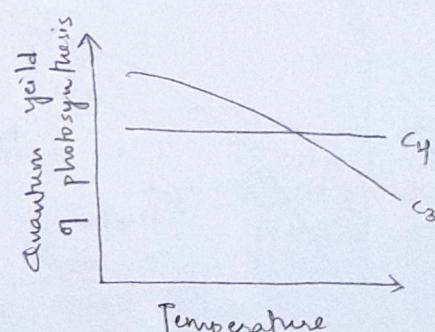
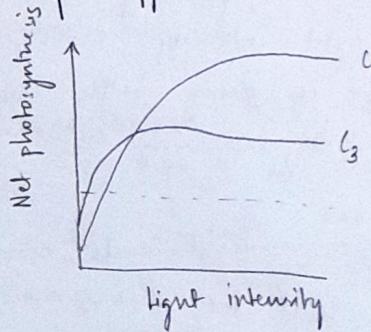
Temperature is important to plants



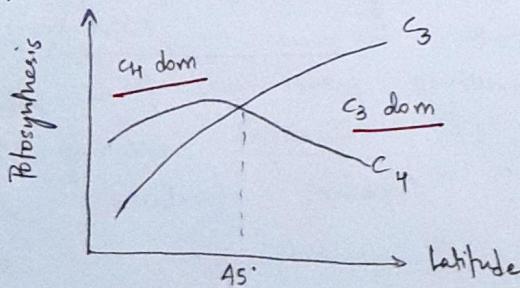
Differential response of photosynthesis & respiration to temperature shapes net photosynthesis with T.
Net P. drops with increase in T above optimal temp.
Also, water loss increases, photorespiration increases & enzymes degrade with increase in T.

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 it's membrane breakdown

Temp. effects: C₃ vs C₄ plants

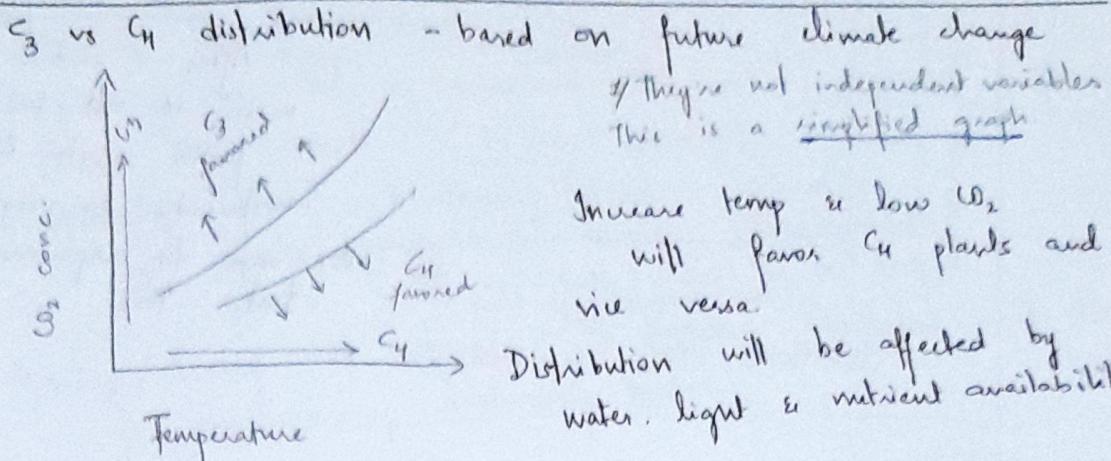


Global distribution

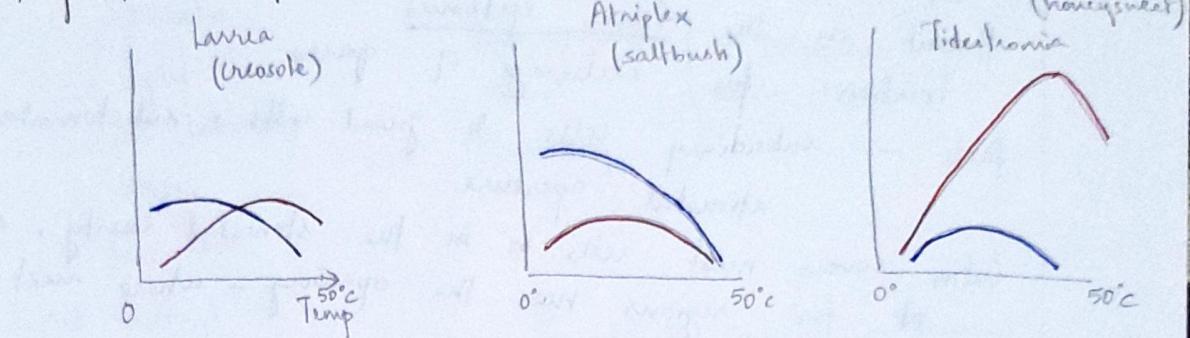


: Predictions based on T

C₄ plants do better at higher T



Temperature response of photosynthesis



- Tidestromia & Larrea : warm-adapted - experience ↑ temp
- Atriplex & Larrea : cold-adapted - experience ↓ temp naturally
- Larrea - it seems like it experiences wide range of T,
 ie greater variability → doesn't acclimate well to cold

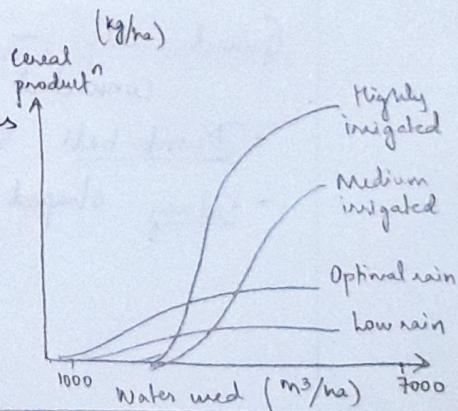
Tidestromia - hot environment
 Atriplex - cool environment

here, we're assuming that the plants can acclimate well to their native T.

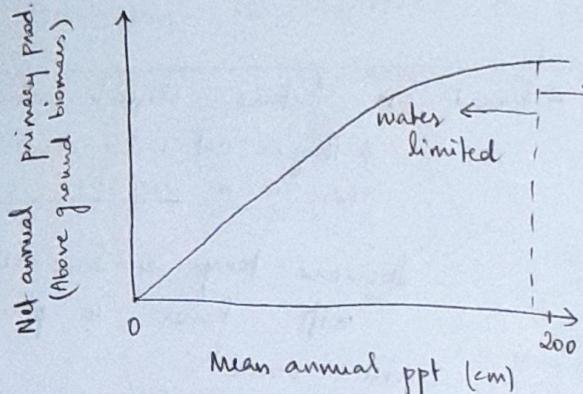
Water and Nutrients

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



Whittaker 1970 - Greenland

Quiz 2 portions -

22/9

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 the substomatal cavity, except pt 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 and stomata opens

Radial micellation out around circumference of pore - cellulose microfibrils radiate

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

- Dumb-bell shaped

- Kidney shaped

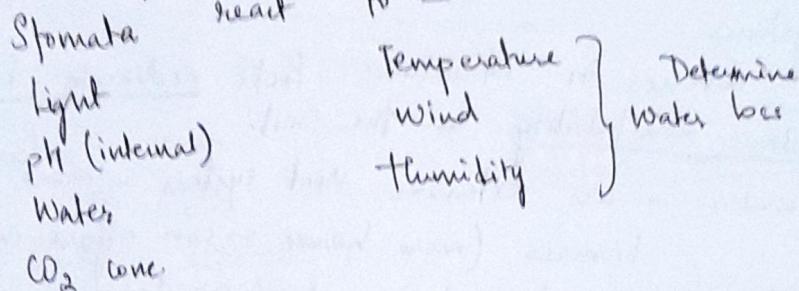
The rate of increase decreases with precipitation
After a certain threshold, water is not the limiting factor - it's likely other nutrients or light.

We can do experiments to test this.

Stomatal pores

- They cover a lot of area : $1000/\text{mm}^2$; 2.8% of leaf SA
- Pores are small : $14\ \mu\text{m}$ (varies)
- Optimally placed & density (sized & spaced)
 - In aquatic plants - it's on the upper side
 - grasses - it's on both sides of the leaf.
- Opening / closing of stomata is tightly regulated - it's like a multicellular hydraulic valve

Regulation of opening / closing -



→ 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 there will be)
Photosynthesis - solutes energy to drive ion-pumps increases internal CO₂ Reduces pH

* Blue light - not related to photosynthesis - directly affects guard cells

- Activates H⁺-ATPase in the membrane
- stimulates breakdown of starch & malate synthesis
- stimulates cellular respiration.

→ Water control

Hydropressive 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 5-15°C)

4. To maintain optimal level of turgidity.

Root systems

Very diverse in structures. Roots adapt 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

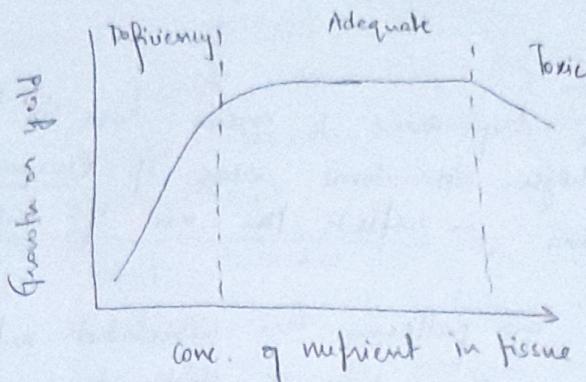
- Life history - stay dormant when water availability is low
Eg: resurrection plant (poikilohydric)
- Deciduousness - shed leaves when water is low
- Changes in leaf morphology - lower SA, sunken stomata, waxy layers, spines, hairs etc (more hairs: less transpir.)
- Root allocation increased - less water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

Mg - chlorophyll

S - proteins (cysteine & methionine) - disulfide bonds

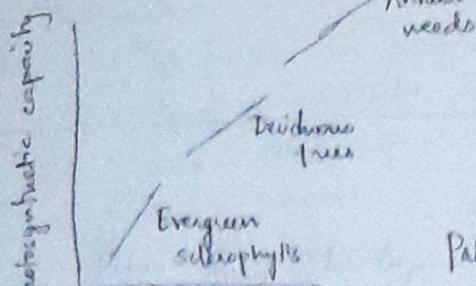
* Micronutrients - required in very low concentrations required in least conc.

Cl, Fe, B, Mn, Na, Zn, Cu, Ni, Mo

They act as co-factors in different enzymes. E.g. metabolism

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

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

Leaf Nitrogen
→ more rubisco

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.

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

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

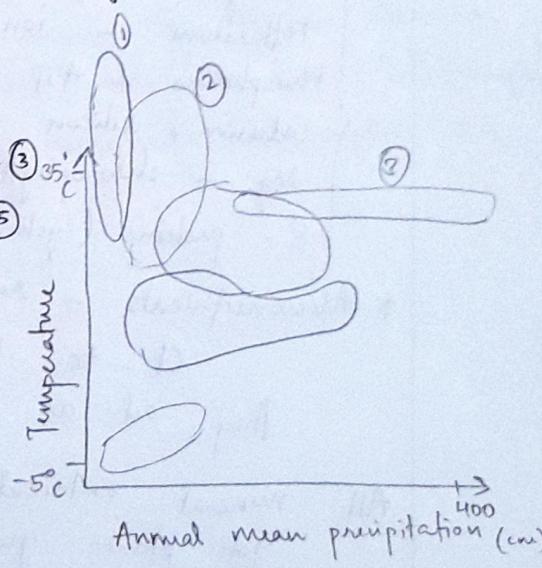
Global productivity pattern

Here, Amazon is SA, equatorial forests in Africa & Indonesia etc are the most productive.

Croplands in US & Europe are less so. This doesn't match with earlier maps - this is mainly because of limitations in water (rainfall) & mainly 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, $[CO_2] = 406 \text{ ppm}$

1960 $[CO_2] = 315 \text{ ppm}$

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 ($> 800 \text{ ppm}$ 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.

26/9

Pigliucci Paper (2002)

* Normothetic knowledge - consists of general laws to understand
 & conquer 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
 Mehl (1978) - problems in 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 alternative 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.
roughly tied to the idea of falsification

Strongly tied to the null hypothesis - stats - Frequentist approach : not the best method
Null hyp - stats - Frequentist approach : not the best method
to understand / prove a theory - not good methods

Bayesian inference

$$P(H_i | D) = \frac{P(D|H_i) \times P(H_i)}{P(D|H_1) \times P(H_1) + \dots + P(D|H_n) \times P(H_n)}$$

TOTAL P. OF DATA

Advantages -

1. Multiple competing hypotheses
 2. Question is posed in a more sensible way
 3. There, 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

Somers paper

Somero papers
 $k_{cat} \propto \frac{1}{T}$, Ea follows same trend, $[E] \propto T$ (to maintain rate)

$$\Delta H = E_A - RT$$

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

High ΔH was paired with high ΔS - enthalpy-entropy compensation
 At a given T , cold adapted orthologs will exist in relatively
 more disordered state than hot orthologs.

$$\Delta S_{\text{halibut}} = -13$$

$$\Delta S_{\text{bind}} = -2$$

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_3 or C_4 plants are more efficient in the given conditions, which might lead to the current distribution.

- C_4 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_4 plants do the same at all temperatures - same quantum yield. But C_3 plants' (which do better than C_4 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_2 increases.

- Leaf area index (LAI) - in the noon overhead sun, if the area of leaf : area of shadow cast by leaf is the same, then $LAI = 1$.
 $LAI = 1 \Rightarrow$ absolutely no shading
 $LAI = 8 \Rightarrow$ self-shaded leaves \rightarrow lower leaves are light-limited
 simply means more number of leaves.

Increased LAI

- Fig 3 - Daily C gain vs LAI
For $10^\circ/5^\circ\text{C}$
- C gain increases with LAI
Rate of increase is larger for C_3 than C_4
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

(30) In B ($30^{\circ}/15^{\circ}\text{C}$) -

- * C_4 plants are more efficient than C_3 : higher T.
- * free, the curve is qualitatively different. After, LAI = 6, the net C gain decreases because of leaves are light limited, & respire more.

In C ($40^{\circ}/20^{\circ}$) -

- * The optimal LAI has decreased - decreases with T.
- * C_3 plant is doing worse because of photorespiration

Study Fig. 4 and Fig. 6.

Latitude : $< 45^{\circ}\text{N}$ - C_4 plants have an advantage

$> 45^{\circ}\text{N}$ - C_3 plants have a competitive advantage

The data in this study (photosynthetic rate) is at the sub-organelle, they calculate daily C gain, quantum yield & make inferences at the individual level and 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
 - * growth forms - grasses form new individuals through nodes.
 - * size
 - * Senescence
 - * integration in modular organisms

Determining population size -

1. Quadrats / transects - for plants in a region

2. Mark - recapture

3. Index of abundance

Mark recapture

Survey 1 - $M = 12$

Survey 2 - $C = 15$

$R = 4$

Total N

soz marked individuals
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

(38) M-R methods - Peterson, Schaubel - closed pop
Jolly — open pop modification

Life history
life cycles of individual describes the stages
that organisms go through -
Birth - growth - reproduction - death

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

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

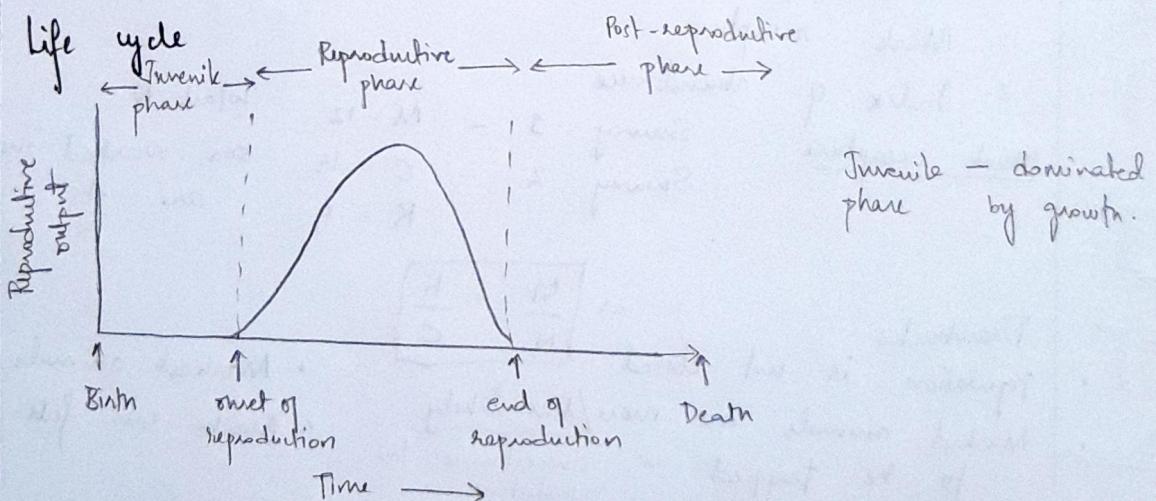
1. Growth & development rates and schedules
2. Timing of reproduction
3. Size at birth or germination
4. No. & size of offspring
5. Age at death
6. Dispersal

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

Semelparity is synchronicity - predator satiation

BUT : Energy and resources are limited!

Energy - resources used for one function can't be used for others \Rightarrow there are trade-offs



Life cycles

Annuals vs perennials

Heteroparity - 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
- Suitable breeding grounds / conditions are rare
- 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 - 6000km)

→ Heteroparous

- Invests lower 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

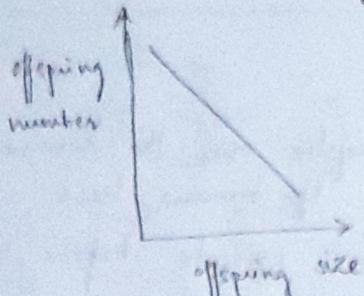
Two factors that influence reproductive strategy -

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.

40
Foundry
There's a trade-off b/w number and quality of offspring



Eg. animals, pine trees

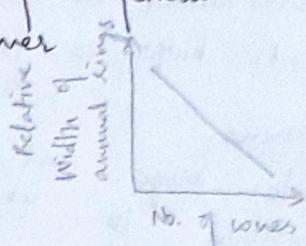
one function, then functions is reduced.

Reproductive trade-offs

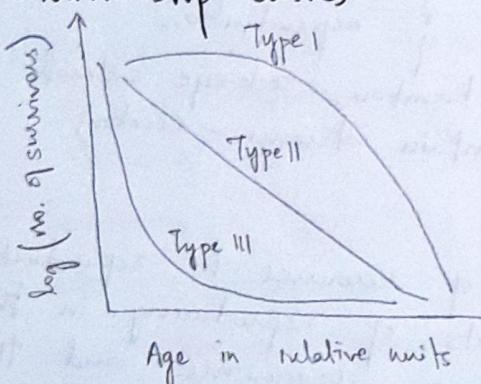
- Reproduction vs. future survival
- Reproduction vs. future growth
- Current vs. future reproduction

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

- Winter mortality is higher for female deer that reproduced than summer
- 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 increases in older age
Eg: Humans

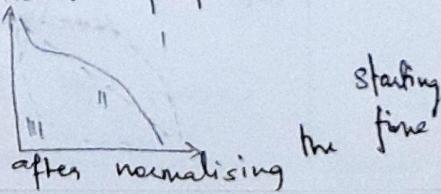
Type II - constant rate of mortality throughout life
Eg. birds, deer, rabbits

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

Leisure - 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
survivorship we can discuss the
ecological strategies that these organisms
 life history 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.
 Greater the investment in offspring, lower the fecundity.
 \uparrow quality \Rightarrow \downarrow quantity.

The different strategies give rise to -

* k-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

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

Opossum example

Life span: 2-4 years
 1-3 mo: dependent on mother

10 mo: maturity

~24 mo: death (killed by predator)

Energy used for:

1-10mo: growth, metabolism, repair

10-20 mo: reproduction, metabolism, repair

- (12) 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 needed out - they accumulate in the population.

27/10

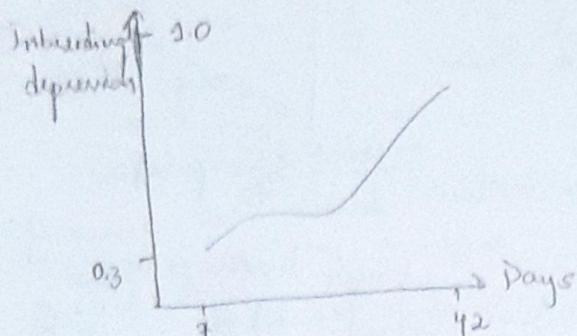
Lecture 19

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.

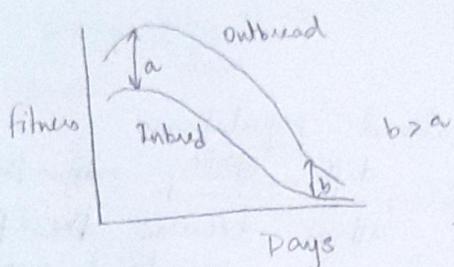
Evidence for MAT

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



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

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



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

The fitness is worse for older mutations, because deleterious mutations accumulate by there

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

→ Antagonistic pleiotropy

G.C. Williams - 1957.

Alleles that increase fitness in old age

fitness in early life but decrease

Evidence: Methuselah homozygous mutant

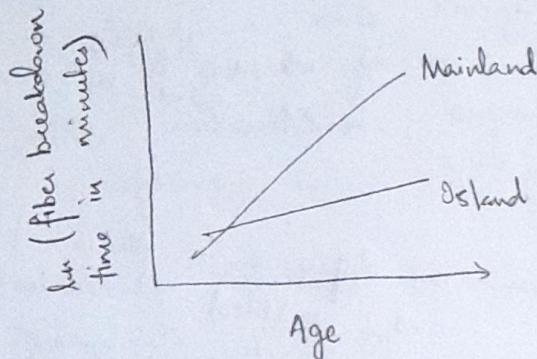
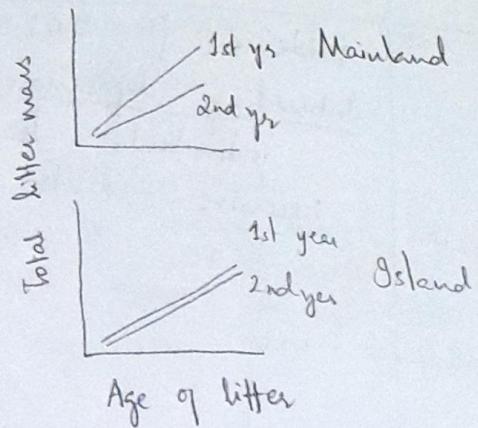
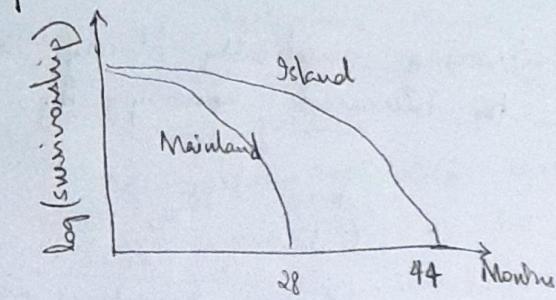
If has greater survivorship than wild type but at the same time, much lower cumulative fertility.

Tradeoff b/w fertility and lifespan.

(44)

Opossums - 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.

28/10

Lecture 20

Intraspecific competition

Nature of interaction

Interaction Type	Competition	Amenalism	Predation / Parasitism	Mutualism	Commensalism	Neutralism
	-	-	-	-	+	-
		Elephant trampling			+	0
						0
						0
						- no interaction

Allelopathic chemicals in plant
but the secretor benefits
or there's too much cost

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 -

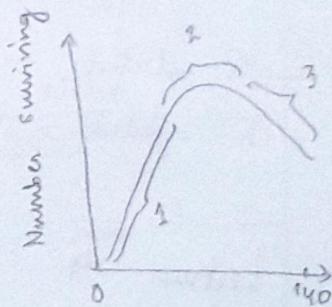
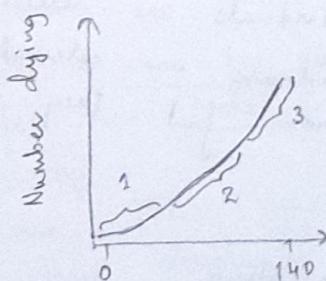
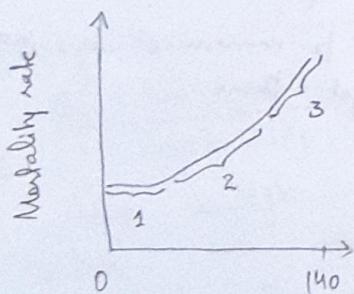
Scramble / Exploitative

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

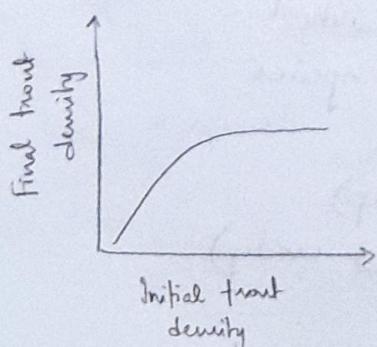
→ Pre-emptive competition
Based on presence ie who came first

→ Density dependent mortality

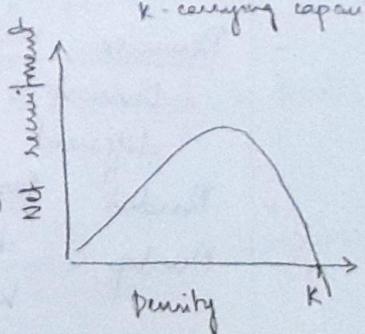
Flour beetles - *Tribolium confusum*



Initial egg number



Perfectly compensating density dependence in fronts



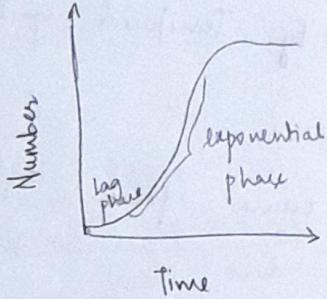
$$\text{Net recruitment} = \text{No. born} - \text{No. dying}$$

Net recruitment : increases, reaches optimum, then decreases.
 If N_{t+1} is -ve \Rightarrow population is declining
 $0 \rightarrow$ no growth in population.

Carrying capacity

If it's determined by the birth and death rate - when they're equal, the number of β 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

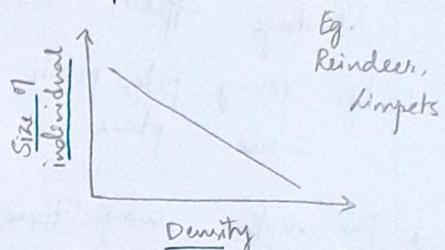
Sigmoidal growth curve



Might not even reach their K .

R -selected - individuals are selected to maximise R
 K -selected - individuals are selected to maximise K , not R
 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.

3/11

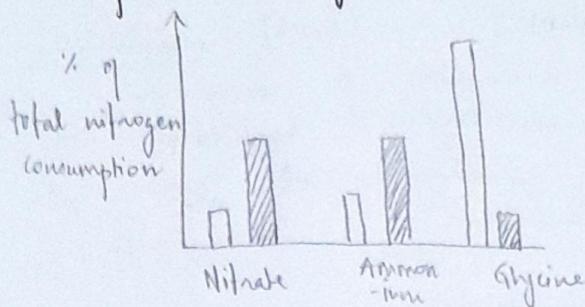
Lecture 24

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



Glycine
 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 competition.

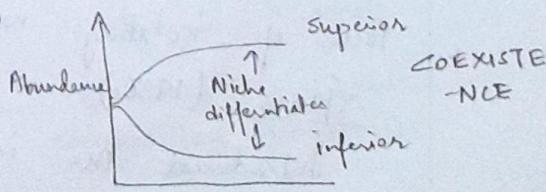
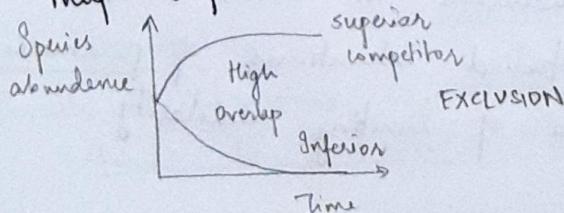
Competitive exclusion

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

They displaced in terms of habitat



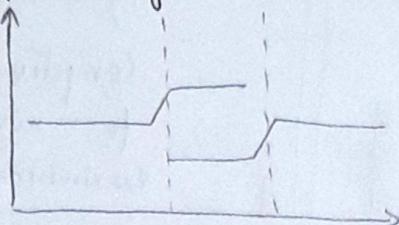
green anole
has been
displaced
by brown

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.

character mean



Example : Galapagos finches - Grants

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

There 3 species - fuliginosa, fortis & magnirostris

- 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. Character 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
- Gause (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)

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

Criteria for identifying competition.

- Competition should explain the distribution & relative abundance of species
- It's necessary to show they use common resource which may provide basis of competition
- There should be evidence that intraspecific competition is occurring based on performance of natural population
- Field manipulations of resources & populations to verify
- 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 use of aquatic vegetation were measured for 8 closely related fish.

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

Warbler feeding zones (Effects 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 (Srilanka 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

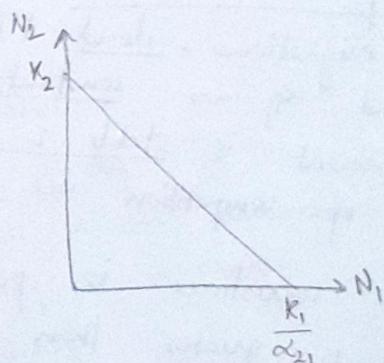
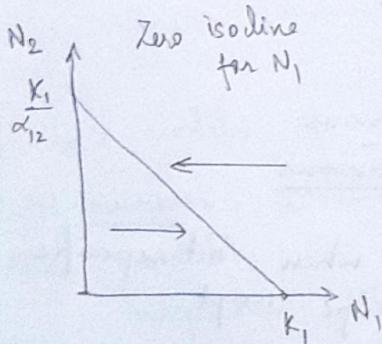
$$\frac{dN_1}{dt} = r_1 N_1 \left[\frac{K_1 - N_1 - \alpha_{12} N_2}{K_2} \right]$$

α_{12} : competition coefficient
Translates individuals of sp. 2 into sp. 1

$\alpha_{ij} N_j$: how much does sp. j utilizes 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 interspecific < intraspecific compt.
- $\alpha_{ij} > 1 \Rightarrow$ intra < inter

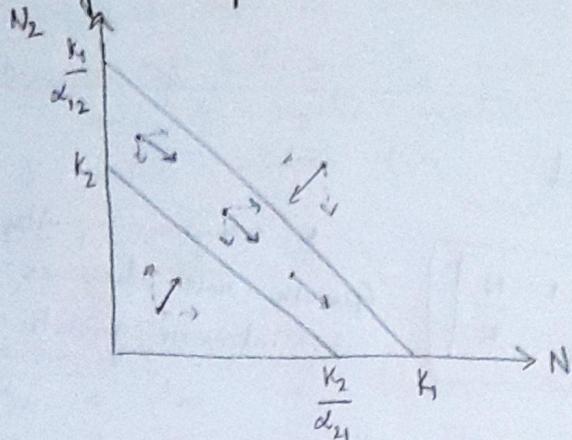
- Zero growth isolines
When $\frac{dN}{dt} = 0$, there's no growth. We find N when $\frac{dN}{dt} = 0$



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

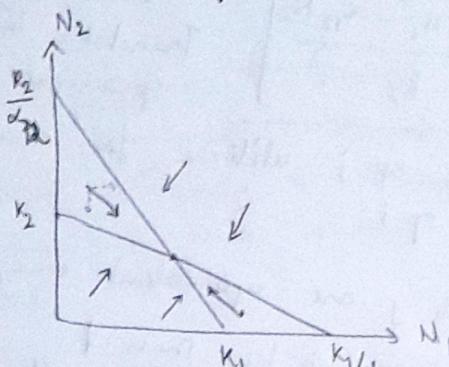
(52)

Arrangement of α isolines.

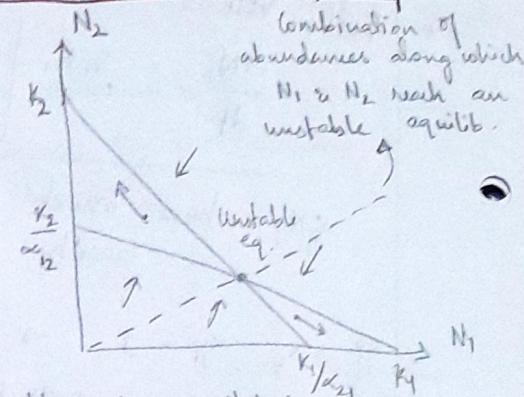


If we're in the region or any region between the two isolines, then we'll always go to K_1 , so that N_2 gets competitively excluded. This is a stable equilibrium.

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

Assumptions of LV model

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

Stable coexistence is possible when intraspecific comp't is greater than interspecific comp't.

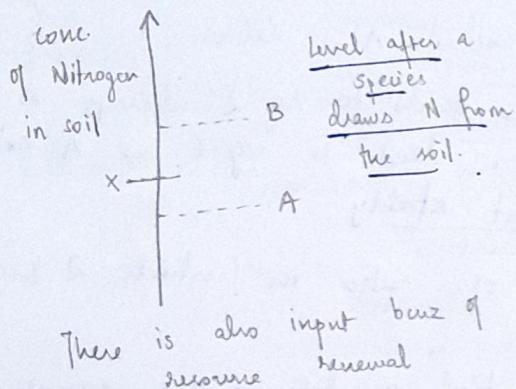
↳ confirm & verify!

Mechanistic models of competitions

- Incorporates resources through rates of utilization
- K and α are represented as rates of 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 in resources
- Supply rates of limiting nutrients
- Population growth rate as a function of nutrient supply assumed to level off due to saturation
- Competition occurs through the effect of each species on the consumed resource i.e. exploitative

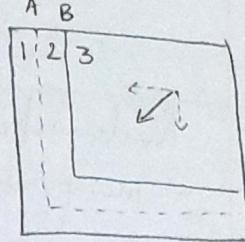
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Lecture 24

11/11/21

Zero isolines for growth

- Region 1 - below min. conc. for both A & B supply rate γ
 \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.

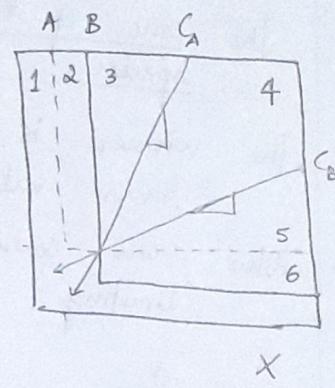
A consumes Y faster/more than X
So Y is limiting for A

B consumes X faster, because X is limiting for it.

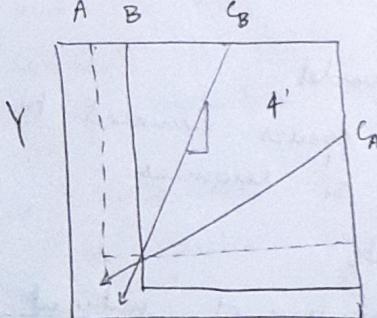
Region 1 : neither would survive

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 extinct4 : both can coexist stablyC_A C_B - consumption vectors of ratio in which 2 resources are consumed.

This assumes that the initial populations are equal.

Limiting Y
X

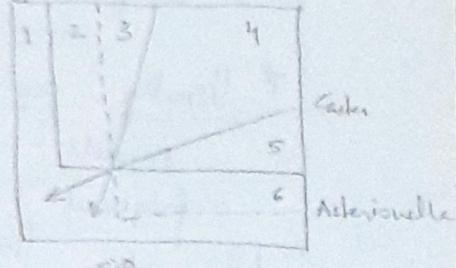
A	Y	X
B	X	Y

Unstable coexistence - 4'

In nature, organisms would be (probably) 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
- 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

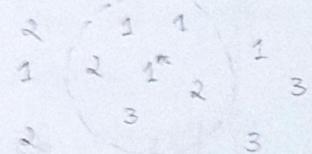
- Previous model worked for phytoplankton where resources are more homogenous
- Doesn't work for land plants where spatial relationships are important to competitive outcome in plants.
- 2 types of models: simulations that keep track of plants spatially
analytic model that captures the essence of spatially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

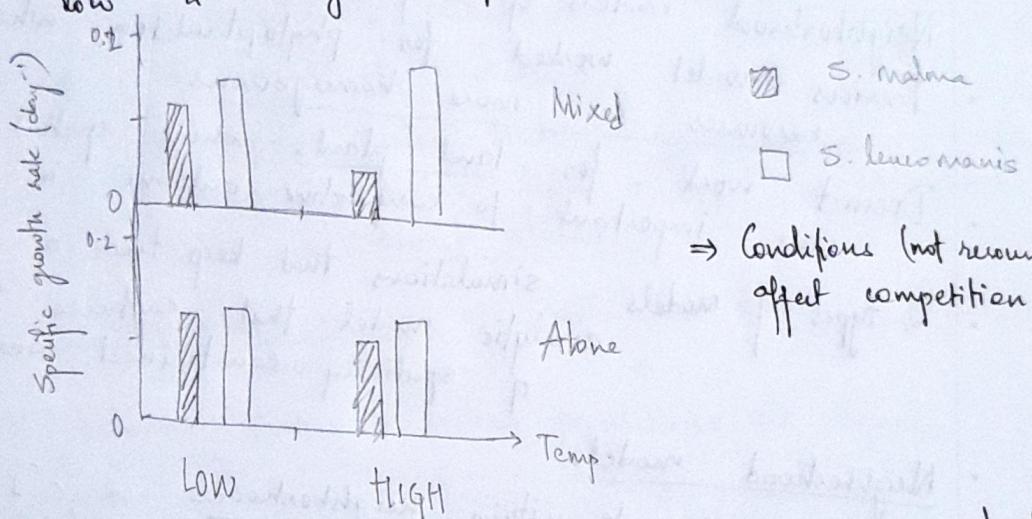


Assumptions of competitive models

1. Isolated populations
2. Stable & homogenous environment
3. Individuals are homogeneously distributed
4. Effect 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 environmental changes keeps the populations frequent 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.



⇒ Conditions (not resources) affect competition

15/11/21

Lecture 25

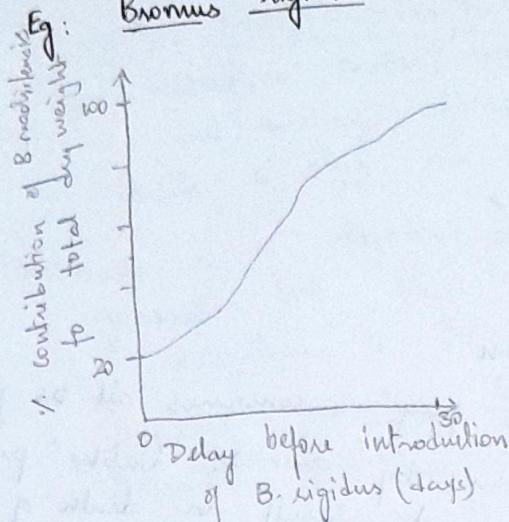
Competition for one resource can affect comp. for other resources

Eg: Root & shoot competition in corn & pea plants

	Control/grown alone	Root compt.	Shoot compt.	Root & Shoot compt.
Biomass	100%	57%	90%	53%

* Below & above ground compt. is not necessarily additive

→ 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
 $Bromus rigidus$ vs $Bromus mediterraneus$



Delay in introduction of *B. rigidus* reduces its competitive ability

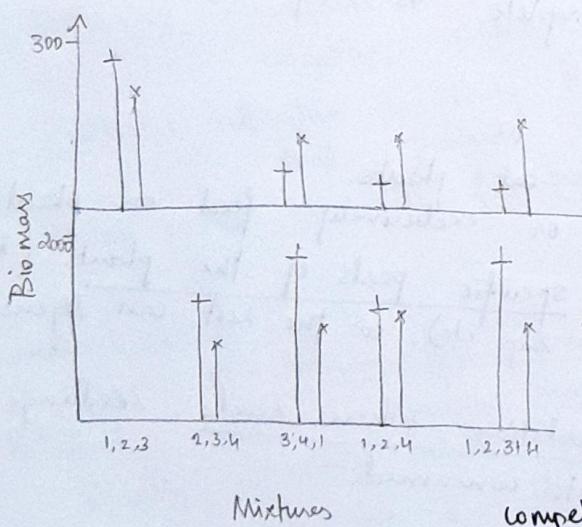
If both start out at the same time, *rigidus* dominates the interaction

→ 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 record is a proxy for intraspecific competition.

⇒ P.a. : interspecific interaction is dominant

S.m. S.m. : intraspecific comp. is dominant.

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

Indirect or apparent competition
Competition

Interference

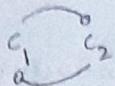
Exploitative

Apparent comp.

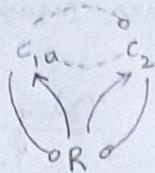
Indirect interaction
via shared
enemy

Indirect interaction
via other species on
same trophic level

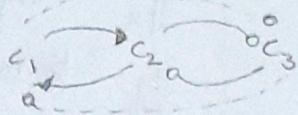
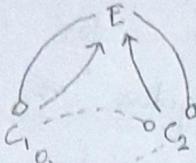
Natural
enemies (P)



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 - eats & eaten belong to same species
4. Parasitism : host provides some resource/nutrition to parasite at a cost. host may or may not 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 in fields
 - 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, digitoxin etc. nicotine,
 - Fruits : attractive & tasty tissues surrounding seeds that promote dispersal
 - Nectar : as reward for pollination.

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

(60)

Parasitism

- * One individual of a species consumes tissues 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 -

folivores : leaf predators	grazers - eat grasses
granivores - seeds	browsers - eat shrubs & trees
frugivores - fruits	

How much do herbivores eat?

n 10% of leaves of forest trees Young leaves are preferred over old

Tundra - 3%
Forests : 4-10%
Grasslands : 10-15%
Rangeland/grazing system : 30-60%

Bottom up limiting resources - water, nutrients, light

Top down - herbivory (but it's 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 from 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 (TSS)

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 -

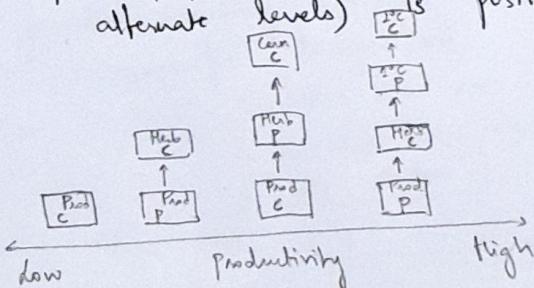
- * { - evolution of defensive compounds
- community composition
- reduce productivity
- affects seedling survival and demography
- seed predation.

Arguments against TSS theory

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

Fretwell's theory (1977)

The trophic complexity
alternate levels)



(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.

(60B)

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 (e.g. buffalos saline & vine). When part of plant is taken away, it alleviates some nutrient limitations for the plant - which increases productivity in terms of biomass.

Oversizing

Increase in livestock since 1950 has led to severe oversizing. The result is deforestation, degradation, deterioration of grasslands, desertification.

Encroachment, burning, lopping etc

Plant defenses - mechanical (thorns, spines)
chemical

Lecture 28

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

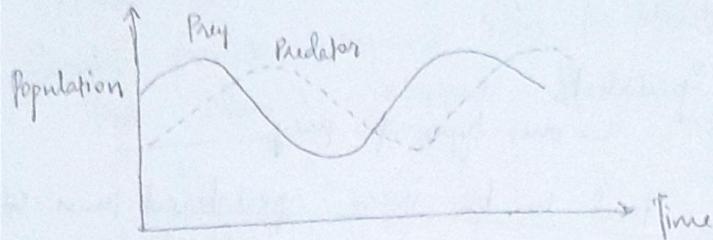
(61)

18/11

Predation

Conspicuous interaction - one individual kill and consume another species

Most thoroughly studied consumptive relationship of high ecological and evolutionary relevance
 Results - predator has little/no effect on prey population
 predator eradicates prey population if goes extinct as a result
 predators & prey coexist dynamically



There are cyclical patterns of predator & prey population numbers. There's a phase shift because there's a lag for reaction/response time of predators w.r.t. prey nos.

Eg: Snowshoe hare & Lynx

Effects of predators on prey

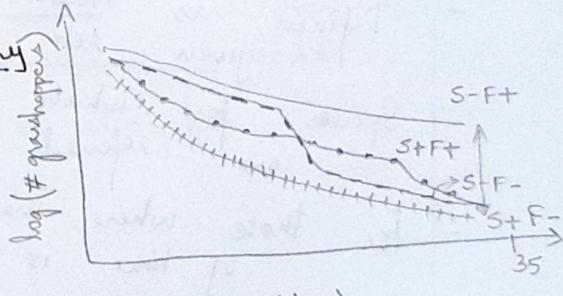
Most direct effect - reducing number of prey
 But we assume that predation is random. If weaker individuals are picked off, then they're demographically less important. \Rightarrow predation might not have that big a negative effect on the population

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.

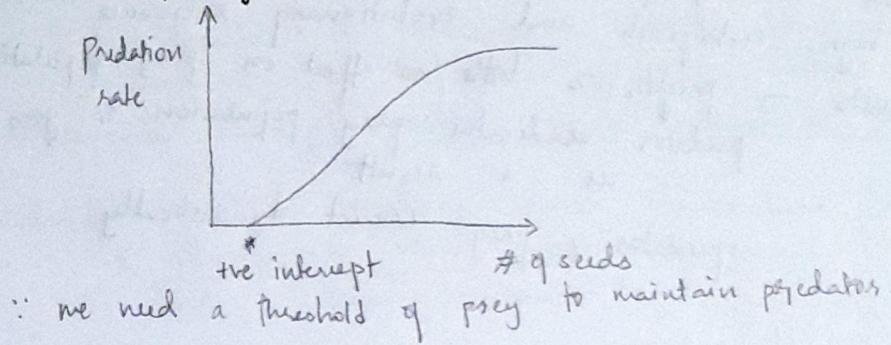


S : spider (predator) F : fertilizers

Comed
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.



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 behaviors of a predator to some "optimal" predicted pattern
- Defined as maximum possible energy return under a 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's different?

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 not all of equal or high energy value

Optimal diet

→ Should predators expand diet to include other prey?

Diet should expand if —

$$\frac{E_i}{(S_i + h_i)} > \frac{E}{(S + h)}$$

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 any energy input.

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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

(64)

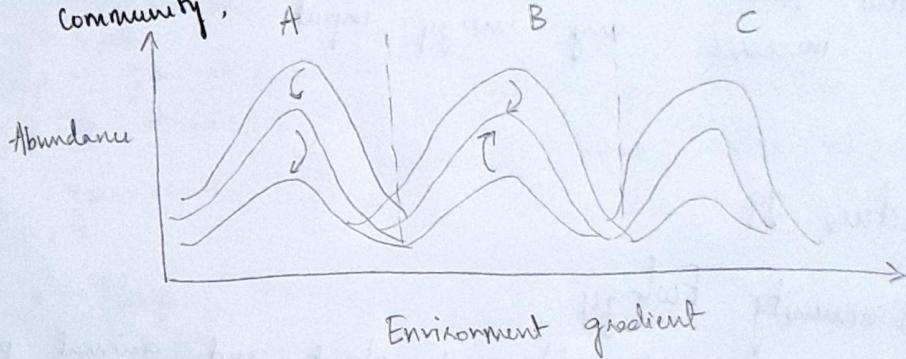
- This field seeks to understand -
- * underlying mechanisms that create, maintain and determine the fate of biological communities
 - * properties of communities and the consequence of variation in these

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

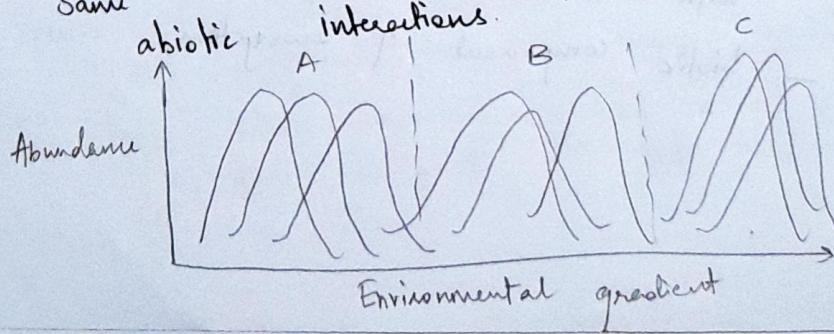
Community function
More than the sum of its parts. Emergent properties -
Community productivity
Community stability
Resilience
Succeⁿsion

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 superorganism.



→ Gleesonian 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 in history/chance
- { dispersal ability
- abiotic condtn & 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
- Spatial/temporal structure
- Richness } No. & distribution
- Abundance } of species
- Diversity }
- { Evenness
- Community similarity
- Trophic levels
- Feeding guilds
- Endemism

→ 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 relation 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 covers.

* Grest, Slope, Valley

→ Temporal structure

Timing of appearance and activity of species.

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

→ Richness and Abundance

↳ abundance of different species / gross abundance
↳ no. of species

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

Eg: Panchmati has lesser species than IISER Pune.

24/11/21

Lecture 30

→ Problem with richness & abundance

Edge species are invasive/toxic, anthropophilic & are everywhere

Doesn't take into account endemicity

May lead to converge 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

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

(67)

Diversity indices

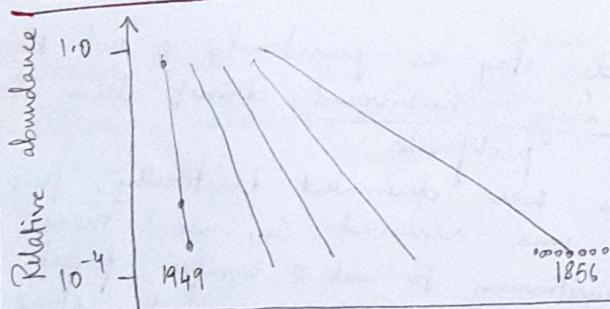
- Combination of richness & abundance, combining them in different ways
- Sensitivities : unevenness & low absolute nos. leads to strange results
unequal collecting/sampling effort
- Common indices
 - Shannon - based on theoretical basis from Signal theory
 - Brillouin
 - Simpson
 - Fisher's alpha - 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



Greater the asymmetry,
sharper the slope of
relative abundance
More even \Rightarrow flatter the curve

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

(68)

Succession

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

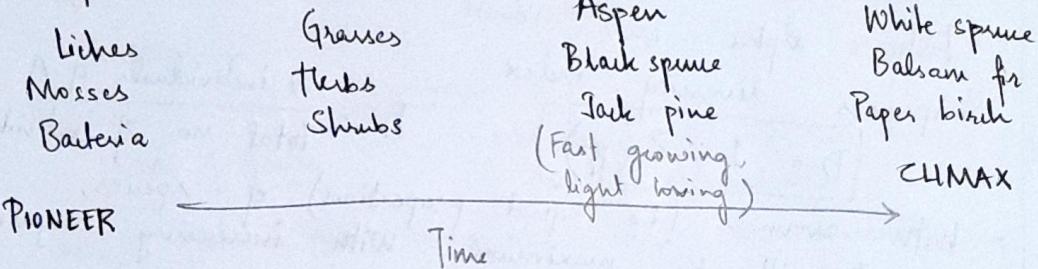
Ecological succession: predictable change in species over time, as each new set of species modifies the environment to enable establishment of other species.

This is virtually ubiquitous.

Early contribution by Clements: analogy of Superorganism & developmental trajectories

* Primary succession

Starts in an area devoid of life (e.g. volcanic island)



* Secondary succession

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

The final successional state of a system represents a dynamic equilibrium b/w progression & disturbance. So it might never reach climax community.

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

In NA, when bison 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. Early - colonization Late - better at compt.
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

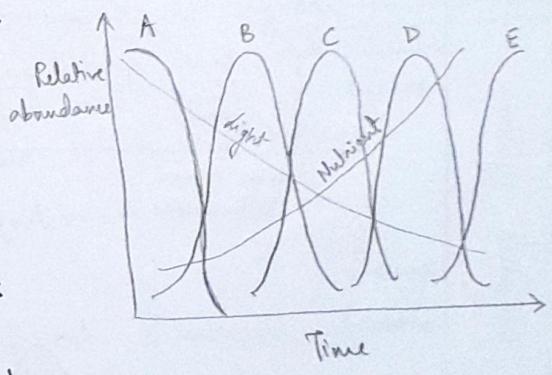
Different nutrients are limiting at different stages

Early ↑ light ↓ nutrients

Late ↓ light ↑ nutrients

So the abundance of species is

determined by relative competitive ability of plants affected by availability of light: nutrients.



(70)

- 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

10/2/2021

before 25/11

Patch dynamics : spatiotemporal view of communities

Habitats are patchy in time & space

Small scale disturbances (tree falls) create gaps & patches

Disturbed gaps are re-colonized

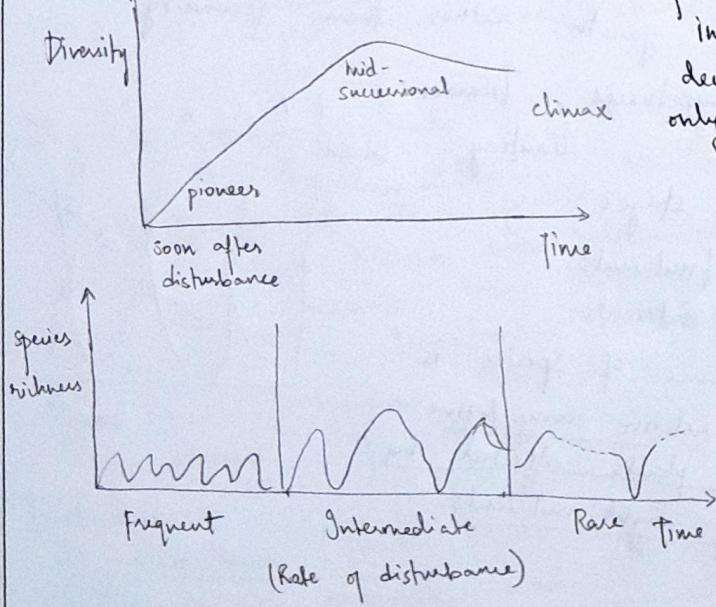
They are important in studying how the community deals with disturbance, how recolonization happens

Dominance controlled system - some species are competitively superior

Founder controlled system - all species have equal competitive ability

Intermediate Disturbance hypothesis - Connell 1978

Dominate
for
this
is
Controlled



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

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 does not change with time since disturbance
 - High levels of diversity can be maintained
- Eg: Great barrier reef

Energy flow through ecosystems

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

Eugene Odum - focused on energy transfer as well as nutrient transfer, so biogeochemicals are important
Wrote an influential textbook ~ 1971

Defining an ecosystem

There 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
(e.g. lake, agricultural field)

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

Contemporary view

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

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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

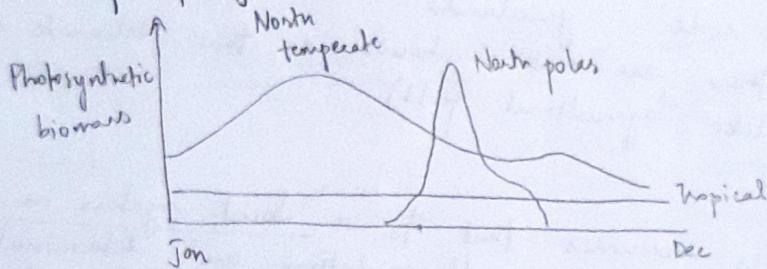
Measuring energy flow

Biomass - measured as dry weight (bcz 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 - O₂ uptake (photosynthesis)
O₂ output (respiration)
Chlorophyll concentration, C-H ratio, transpiration, remote sensing

Map of global productivity



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

Plants use up to 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% humans: 0.01%

Mammals -	Livestock: 60%	Birds - poultry: 10%	Bindi - wild: 30%	Wild animals: 4%
	Sixty mammals	30% avian mammals	30% plants	4% fish
	induced by -			
	83%	20%	50%	15%

Net primary production in ecosystems

Swamp & marsh > Tropical > Temperate forest > Grassland ... >
 Tundra > Desert
 Aquatic - (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

Lecture - 29/11

→ marine, resist molasses
 filter-feeders

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 more tolerant?

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

- Adult 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

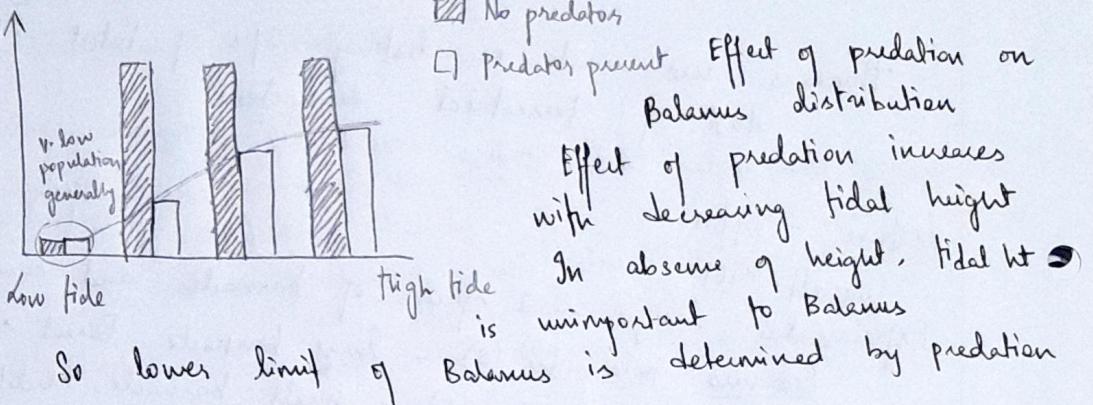
Abundance distribution graphs -

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.

(44) 3. Predation is not very important for dist. of Chthamalus, since (that's) 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.

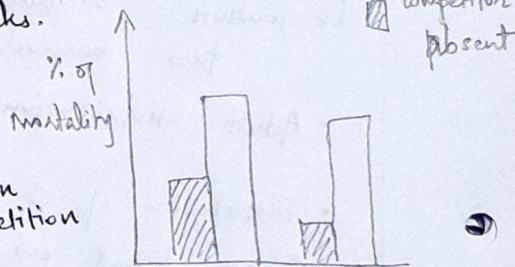
Lower limits of distribution



Chthamalus lower limit

the took rocks with C from higher tidal zones and moved them to lower levels, and allowed Balanus to colonize some of the rocks. Then removed 8 from half of the rock.

Balanus limits Chthamalus distribution and abundance through competition



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

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

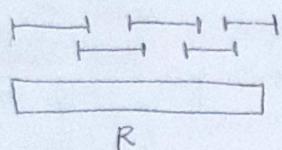
Resource partitioning (Eq. theory)

↳ 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

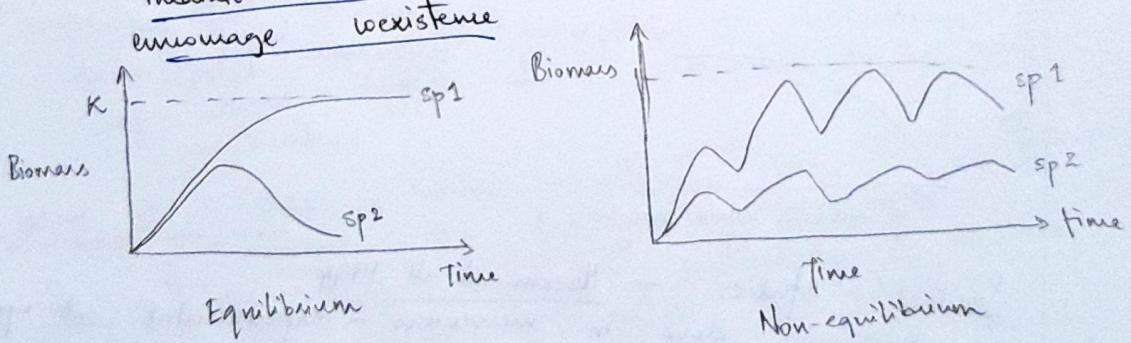


We can increase the number of species by -

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

Non-equilibrium theories

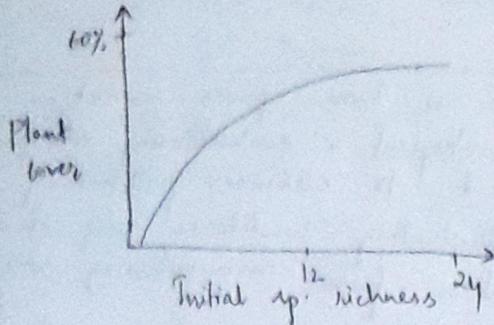
Processes such as stress, disturbance or predation can mediate resource availability (prevent comp. exclusion) and encourage coexistence



Non-equilibrium theory - intermediate disturbance hypothesis

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Biodiversity is related to ecosystem productivity - Tilman 1996



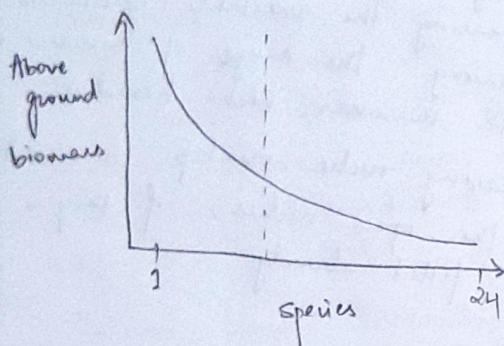
Increases sharply initially, then plant cover plateaus with further increase in richness

Lecture - 1/12

11/12

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

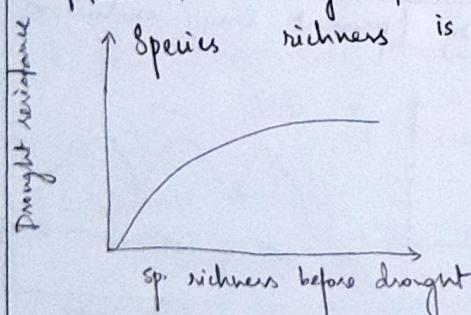
Perhaps this increase is because increased species would be able to utilize nutrients better, more efficiently. Also monocultures are more susceptible to disturbances. Also - more species - higher chance of mutualistic interaction



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

Assignment Q.

Tilman & Downing 1992



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

Seminal
studies
with

studies - Naeem et al 1994

was done in mesocosms - experimental set up decomposes, 1^o producer, 1^o & 2^o consumers. They had high, medium and low biodiversity systems

* W_a flux

- highest in high diversity
lower in low & mid diversity

* % change in plant cover increase w/ increase in 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 richness.
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 v. important.

Hooper et al. - biodiversity some ecosystem functions, Srivastava & Vellend - for functionally important species identifying can be more useful

- Balvanera et al. 2006 - meta-analysis
446 measures of biodiversity across (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 manipulated trophic links b/w elements measured

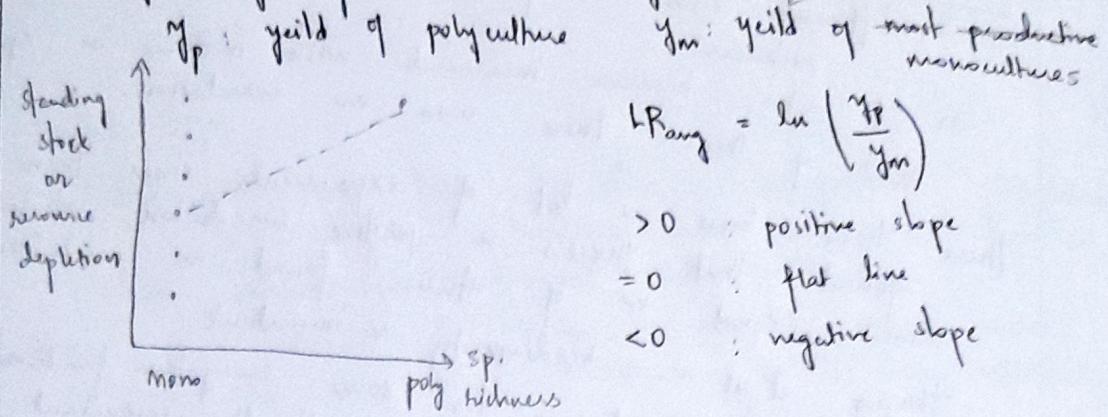
Insurance effect
Monocultures are more susceptible to disturbances. So having more species allows ecosystem to be more resilient.

Worm et al. 2006 - marine ecosystem
They measured the fish catch measurements
They had different measures - productivity, % recovery, average catch etc against sp. richness
They increased with increase in richness (linearly)
Coefficient of variation (inverse of stability) decreases with increase in richness.

93 studies - 175 experiments

- direct manipulation of ≥ 3 species
- 4 trophic groups
- Response variables: standing stock
resource depletion

LR_{avg} : log response ratio on avg mean



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

So, polycultures are more productive and sustainable/efficient

Resource depletion is ≈ 0 for plants & herbivores - may not have a great effect

Broadly, we can say biodiversity increases ecosystem function

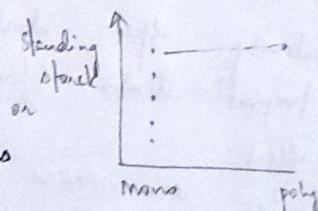
LR_{max} : max. log response ratio

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 - $LR_{max} \approx 0$ for plants

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

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

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

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. It's 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