

Lecture 1: Distributional Aspects of Biodiversity

Distribution of abundance: Why are organisms found where they are?

Organisms found in places where they can thrive

- Need certain resources and conditions (**abiotic factors**)
- **Resources** exhaustible (ex. nutrients and space)
- **Conditions** not exhaustible (ex. temperature and salinity)
- Conditions vary across space and time → **gradients**
- Organisms have ranges of tolerances along these gradients
- “Performance” of organism function of gradient
 - o Very bad conditions = death
 - o Bad conditions = survival (bare minimum)
 - o Good conditions = growth
 - o Excellent conditions = reproduction

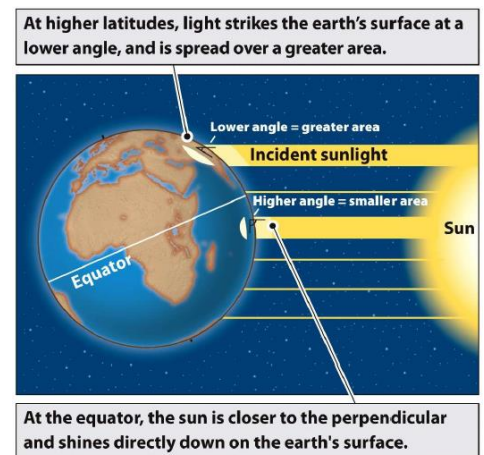
Important factors include (terrestrial):

- Plants – temperature, soil moisture, nutrients (esp N, P, K), disturbance (esp fire), herbivory, disease, pollinators, seed dispersers, fungi, etc.
- Animals – food/water, temperature, habitat quality (ex. cover, nesting sites), predation, disease

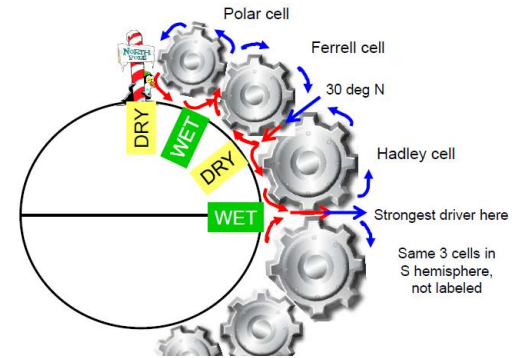
***Animals tend to follow plants**

Temperature and precipitation patterns: latitude

- ↑ latitude = ↓ solar energy (cold)
- ↓ latitude = ↑ solar energy (warm)
- Solar energy heats up surface of land/water
- This absorbed energy is released and heats up atmosphere
- **Adiabatic process**: warm air rises → cools → water vapour condenses → precipitate
- Equatorial region warmest and rainiest (explains rainy tropics)
- Once air rises, pushed N/S of equator
- At about 30° N/S, air no longer pushed up by warm air (b/c ↓ solar energy)
- Air descends and warms → dry b/c precipitated in tropics (explains deserts at 30° N/S)
- This circulation = **Hadley cell**
- Other atmospheric cells cause patterns in precipitation

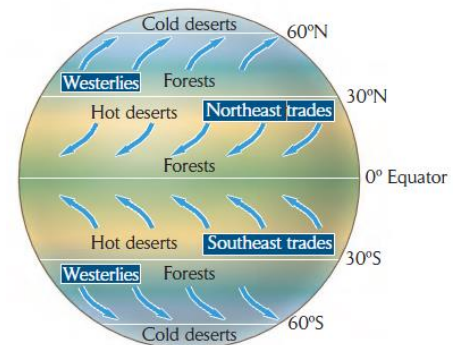
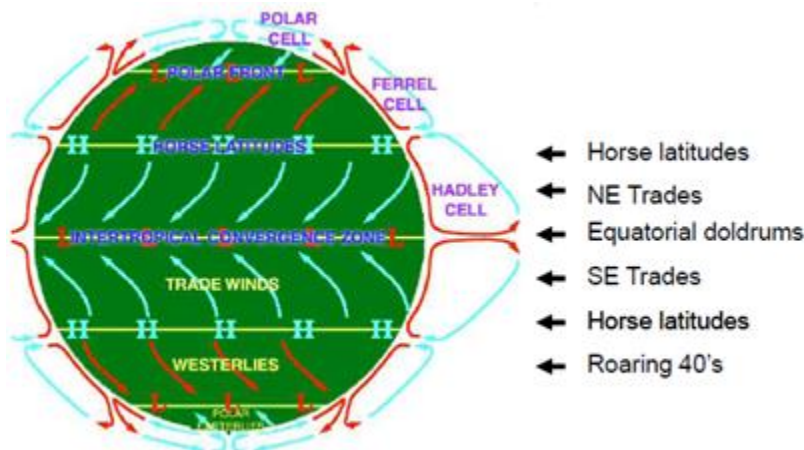


- **Ferrell cell**: air descends and warms, adiabatic process again at about 60° N/S (explains temperate forests)
- **Polar cell**: dry air moves to polar regions
- ∴ Temperature and precipitation function of latitude
- **Intertropical convergence zone**: where N/S tropical air meets, more warm air cycles through Hadley cells than other cells (explains why so rainy and humid)
- Since globe on tilt, convergence zone shifts seasonally causing dry seasons in some parts of tropics → mostly Asia (“monsoonal seasonality” and Central America, little seasonality in South America)



Wind patterns: atmospheric cells and Coriolis effect

- Atmospheric cells cause winds to move N/S
- Coriolis effect: earth spins on axis and causes winds to move W/E
- B/w 30° N/S, air moves towards equator (intertropical convergence zone) and Coriolis effect causes air to move from east to west = **Easterlies** or **Trade Winds**
- Trade winds strong and reliable (i.e. for sailing)
- B/w 30° and 60° are **Westerlies**
- **Horse latitudes**: border b/w Trades and Westerlies, winds generally weak and unpredictable (i.e. ships get stuck, throw off animals to be lighter)
- **Equatorial doldrums**: at convergence zone, where air goes up (not really N/S) ∴ weak
- Note: N Westerlies weaker than S Westerlies b/c earth on tilt, also south has less land to regulate winds (see below) → S Westerlies aka **Roaring 40s**

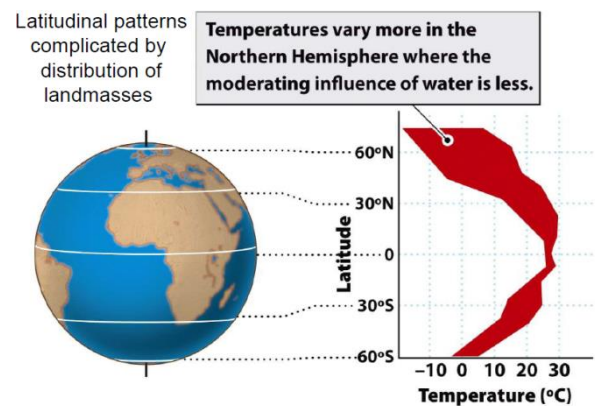


El Nino events

- Trade winds decrease, surface currents follow suit
- Warm water covers ocean surface in tropics
- Leads to high precipitation and flooding in N/S America, even Europe
- Abnormally wet conditions → rodent population boom → disease
- Warm water stays in these parts, no cold water brought in to bring in phytoplankton (main food supply) → marine life die
- Leads to drought in Australia, Indonesia, parts of Africa

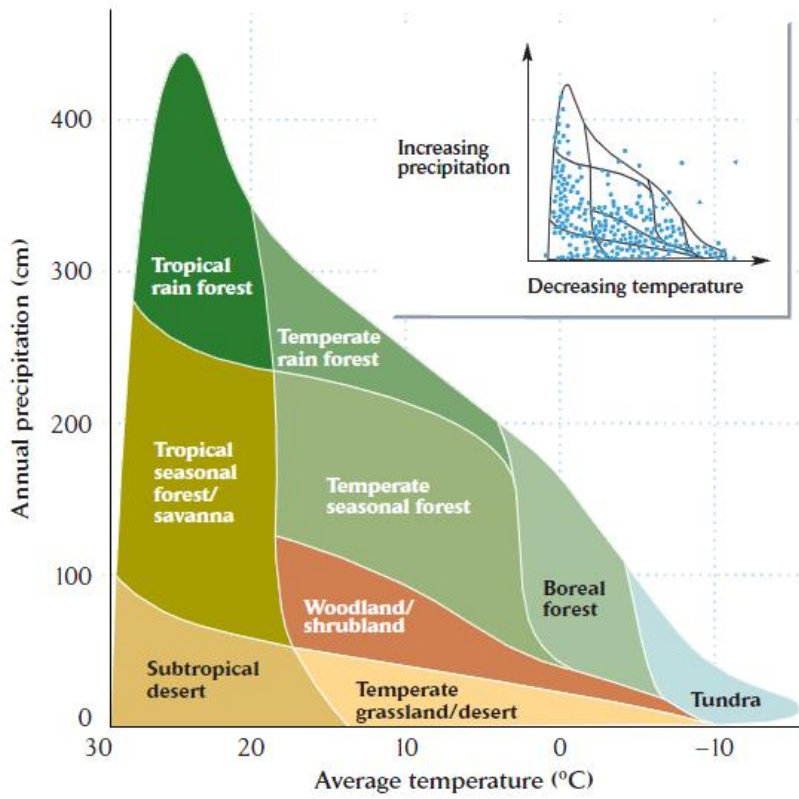
Influence of land forms on climate

- Water resistant to thermal change, can absorb/release a lot of thermal energy
- **Maritime climates moderate** → water provides thermal regulation
- **Continental climates extreme** → no water to provide thermal regulation
- Ex. delicate crops (grapes, cherries) grown near bodies of water (ex. Niagara, Long Island) b/c water moderates temp and prevents from freezing
- Temperatures vary more in N hemisphere b/c less water, more land
- Mountains have rain shadows: air approaches mountains gets pushed up → precipitates (adiabatic cooling) → as air goes over and down mountain, dry and warms up (adiabatic warming)
- ∴ windward side: wet, ↑ vegetation
- ∴ leeward side: dry, ↓ vegetation



Latitude determines biomes

- ↑ moisture and temp = ↑ vegetation growth and stature
- Major types of vegetation = **biomes**
- ∴ Biomes reflect local climate



Biome	Location	Temperature	Precipitation	Vegetation	Notes
Tropical forest	near equator	hot	very high	evergreen tropical forest, herbaceous ground vegetation	little seasonality
Savanna	transition b/w tropical forest and desert	hot	summer rainy season	grasses, scrub, small trees	vegetation maintained by fire
Desert	around 30° N/S	hot	low	perennial shrubs	variable desert climate (ex. rain shadow deserts)
Mediterranean	30-40° N/S	hot summers cool winters	dry summers moist winters	frost-sensitive shrublands and woodlands	vegetation maintained by fire
Grassland	interior of continents	warm/hot summers cold winters	varies, highly seasonal	grass prairie	vegetation maintained by fire
Temperate forest	mid-latitudes	moderate climate with winter freezing	high	deciduous trees	
Coniferous forest (boreal)	higher latitudes	cool summers cold winters	varies	evergreen trees, needle-leaved	
Tundra	near poles	very cold	low	moss, lichen, small tightly-packed shrubs	

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Lecture 2: Species Ranges and the Physical Challenges of the Environment: Heat Balance

Relationship between geographical and physiological ranges

Geographical ranges

- Distribution ultimately limited by tolerance and geographical ranges
- Organisms' reactions occur at optimum temperature/osmotic pressure
- Mechanisms for **homeostasis** evolved to challenge hostile environments
- Maintenance of homeostasis requires energy
- Geographical ranges determined by:
 - o Climate/vegetation (i.e. biomes)
 - o Behavioural habitat selection
 - o Other organisms (friends, enemies)
 - o Ecological versatility (transcending biomes) → **generalists**

Physiological ranges

- Mainly heat balance (tolerance)
- Exchange of heat through:
 - o Radiation
 - o Conduction: direct contact (ex. feet lose heat to ground)
 - o Convection: transfer by fluid (air, water)
 - o Evaporation: efficient cooling from wet surfaces
 - o Redistribution: circulatory system redistributes heat from core to appendages
- Heat balance affected by:

1. Size and shape

- SA and V important (SA → equilibration rate, V → provides inertia)
- ↓ SA/V ratio = conserve heat (spherical shape)
- ↑ SA/V ratio = heat loss (flat shape)
- **Bergmann's rule** (size): homeotherms bigger size at colder latitudes (to ↓ SA/V)
 - o Ex. polar bears biggest bears
- **Allen's rule** (shape): appendages shape reduced at colder latitudes (to ↓ SA/V)
 - o Ex. cold climate rabbits have reduced ears
- Sometimes particular shapes (that go against Allen's rule) needed for function → **trade-offs**

2. Insulation

- Fur
- Feathers (adjustable insulation)
- Blubber (for aquatic animals b/c hair would cause drag)

3. Arrangement of arteries/veins

- Appressed arteries/veins → conserve heat
- Separated arteries/veins → shed heat
- Countercurrent flow maintains gradient (heat always flowing from outgoing blood to incoming blood)

4. Vascularization in appendages

- Enhances convective cooling
- Heat transferred through blood vessels
- Ex. warm climate rabbits have lots of blood vessels in ears (↑ vascularization) to cool rabbit

5. *Evaporation*

- Sweating
- Panting
- Licking themselves
- Spraying water on themselves

Types of thermoregulation

Poikilotherm

- Cannot generate own heat
- Body temp fluctuates (conforms to outside environment)
- I.e. cold-blooded animals (fish, amphibians, reptiles)
- Employ behavioural thermoregulation
 - o Ex. moving b/w areas w/ ↑ or ↓ temp
 - o Ex. changing body position to adjust heat exchange
- Less active, but lower metabolic rate
- Can survive in resource-poor environments (require less food/energy)

Homeotherm

- Generate own heat
- Body temp does not fluctuate as much
- I.e. warm-blooded animals (mammals, birds)
- Employ physiological thermoregulation
 - o Ex. isometric contraction of skeletal muscles (shivering)
 - o Ex. evaporative cooling (sweating)
 - o Ex. dilation of surface blood vessels → promote heat loss
 - o Ex. catalyzing brown fat for heat production (not ATP synthesis)
- Physiological thermoregulation requires energy → metabolic rate ↑
- Also thermoregulate behaviourally, but not as dependent as poikilotherm
- More active, but higher metabolic rate
- Limited habitat choices (needs constant food/energy)

Lecture 3: Physical Challenges of the Environment for Animals, Emphasis on Trade-Offs and Alternatives

Trade-offs

- Involve **cost** and **benefit**
- **Fitness gains offset fitness costs**
- All organisms riddled w/ compromises dictated by trade-offs
- Ex. Weasel shape is paradoxical
 - o Long, thin, short fur → suitable for warm weather
 - o Lives in cold weather, active predator
 - o Shape/lack of fur allows better predation → can fit into narrow burrows where prey live (ex. pocket gophers)
 - o ∴ Fitness gains of being good hunter offset fitness costs of expensive metabolism

Constraints

- **Natural selection** expected to produce perfect organisms, however it doesn't
- Two reasons:
 1. Trade-offs (being good at x offsets being bad at y)
 2. Constraints (organisms similar to parents)
- Natural selection builds on what is already there
- I.e. tinkering (yes), fundamentally fresh redesign (no)
- ∴ Natural selection limited

Extreme water stress: example kangaroo rat

- Lives in desert, can survive w/ little water
- Some adaptations that allow them to live in dry environment
 - o Anatomy → bipedal, less heat gain from ground
 - o Physiology → super-efficient kidneys (allow urination of solutes w/ minimum water), metabolic water sufficient (biochemical breakdown of fat molecules to water)
 - o Behavior → nocturnal, spend hot days underground
 - o Cache seeds underground, recapture water vapour from exhalation

Evasive behaviours

- **Dormancy** → allows minimal metabolism (ex. hibernation, estivation, seeds, cysts, eggs, pupae, torpor)
- **Nest/den** → protective microhabitat
- **Storage of food**
- **Migration** to mild (more favourable) climate
- Hibernation and migration usually driven more by food supply than abiotic stress (mammals/birds can survive cold weather)
- Ex. garter snakes → underground den w/ other snakes to keep close/warm during winter
- Ex. squirrels/chipmunks → extensive feeding during summer to build up food energy storage during winter, have brown fat (extremely good energy source)
- Ex. muskrat → above water nest during winter, don't hibernate but leave nest to swim/eat fish

- Ex. bluebirds/hummingbirds → migrate
- Ex. crossbill → specialist on conifer seeds (available year round)
- Ex. gray jay → generalist (can eat anything), opportunistic and flexible behaviour
- Remember birds can get through winter if they have food source
- Ex. clark's nutcracker → cache seeds, hides in trees and can find next year
- Ex. pika → dries summer plants for winter consumption

Conclusion: physiological ecology of animals

- More than just **physiology**
- Includes **anatomy** (size, shape, insulation, vascularization)
- Includes **microanatomy** and molecular variation
- Includes **behaviour** (parental care too)
- Adaptations work together in coordinated ways
- Such that physiology and behaviour work together (ex. even if good physiology for desert, can't survive if behave in stupid way)
- Diverse solutions for common problems (ex. cold)

Lecture 4: Physical Challenges for Terrestrial Plants, Emphasis on Trade-offs and Alternative Lifestyles

Plant physiology

- Solve problems by growth and development, not behaviour (cannot evade stress by moving)
- Plants are autotrophs → make own food
- Net photosynthesis = gross photosynthesis – respiration
- $\text{CO}_2 + \text{H}_2\text{O} \leftrightarrow \text{O}_2 + \text{carbohydrates}$
- Need: light, gases, water, ok temperature, osmotic balance, enzymes, dissolved nutrients, etc.

Carbon balance

- Photosynthesis happens in leaves
- Size and shape important → SA/V ratio
- Leaves have ↑ SA/V ratio
 - o **Costs:** overheating (denatures enzymes), water loss through stomata
 - o **Benefits:** harvesting light and CO_2
- Plants keep cool by growing in shady habitats or evaporative cooling (opening stomata)
- **Stomata** controls **gas/water exchange**
 - o Open → water loss, but evaporative cooling
 - o Close → water conservation, but no gas exchange ∴ photosynthesis shuts down, plant stops growing
- ∴ Trade-off between water conservation and rapid growth

Microphyllly: adaptation to deserts



- Desert vegetation = fine grained, small leaves (“**microphyllly**”)
- Microphyllly good for deserts b/c ↓ SA = less overheating
- Ex. Palo verde → microphyllly, photosynthetic bark
- Ex. Prickly pear → extreme microphyllly, no leaves but big flat pads (modified stems)
 - o Pads all oriented in one direction, away from sun when its hottest
 - o Also developed spikes to deter herbivory
- Ex. Cacti → extreme microphyllly, no leaves at all
 - o Have extensive shallow roots → good for seasonal rainfall in deserts, can absorb massive volumes of water and store for dry seasons (succulent tissue)
 - o Accordion shape → allows plant to expand shape when storing water



Deciduous: adaptation to cold/dry

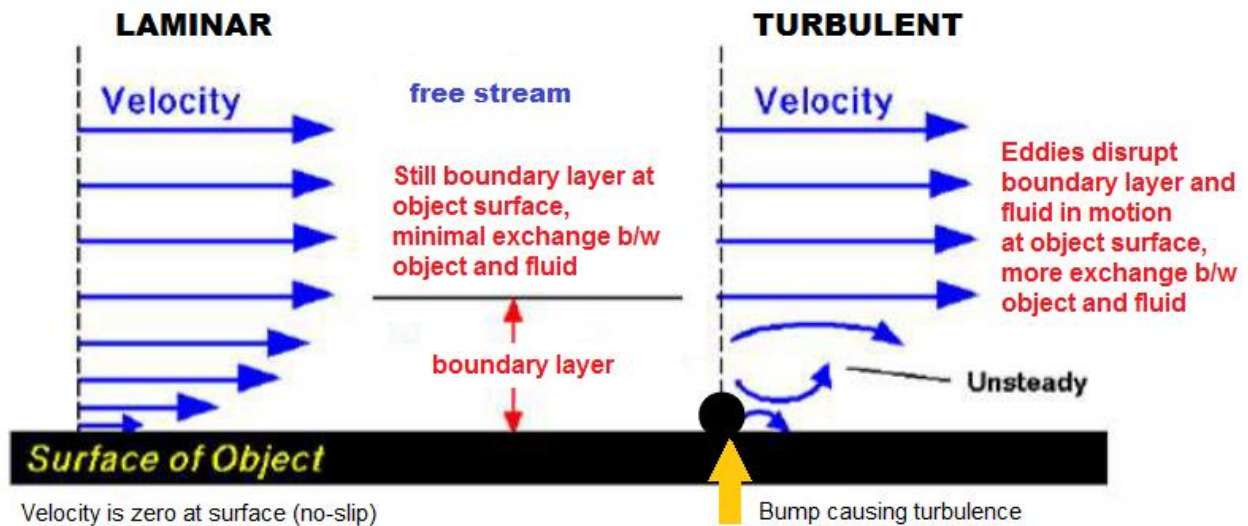
- **Deciduous** = drops leaves when cold/dry to reduce water stress and tissue damage
- During winter, no water and too cold to photosynthesize
- If plants try to keep leaves, leaves would be subject to damage from wind, ice, etc.
- More economical to drop leaves, even if have to regrow them in spring
- *Evergreen ≠ conifer (evergreen is leaf behaviour to keep leaves, conifer is type of leaf)

Schlerophyll vs. mesophyll leaves

Schlerophyll	Mesophyll
<ul style="list-style-type: none"> - Small leaves - Thick needles/scales - ↓ SA/V - Tough, leathery - Typically evergreen → last several seasons - Ex. coniferous trees (pines, firs, spruces) 	<ul style="list-style-type: none"> - Large leaves - Thin, papery, flexible - ↑ SA/V - Flimsy, fragile - Typically deciduous - Ex. hardwood trees (maples, oaks) 

Benefits of schlerophylly

- Leaf shape influences gas exchange through laminar or turbulent flow
- Schlerophylly is **turbulent flow**
- Turbulent flow over bumpy shapes → produces circular, unsteady flow of air (“**Eddies**”)
- ↑ **Turbulence** = ↑ **gas exchange for leaf** → ↑ **cooling**
- Turbulence can be ↑ by zigzag edges, holes
- Laminar flow over smooth shapes, constant smooth flow of air can cause “boundary layer” where minimal air flow at surface → ↓ gas exchange = ↓ cooling
- Sometimes plants have diff leaf shape → more laminar shape for leaves in shade, more turbulent shapes for leaves in sun



- Another adaptation to heat is nurse tree effect → smaller tree shaded by another tree

- Ex. saguaro seedling sheltered (shaded) by palo verde until grows (\uparrow SA/V)

Schlerophylly paradox

- Schlerophylly leaves thrive in many diff environments:
 - o Boreal forest \rightarrow very cold, moist
 - o Pine barrens \rightarrow hot, dry/sandy soils
 - o Maine bogs \rightarrow wet, acidic
 - o Mediterranean heaths \rightarrow very hot, dry
- How can leaves survive in all of these?
 1. Small leaves (\downarrow SA/V) \rightarrow good for dry
 2. Spruce-fir growth form sheds snow at high latitudes, winter-green needles allows photosynthesis year round \rightarrow good for cold
 3. Evergreen habitat conserves nutrients (esp N) in poor soils \rightarrow good for all

Epiphytes

- Grow on trees, don't have roots in soil \rightarrow water/nutrient shortages
- Tend to grow in rainy habitats
- Other strategies include: sponge (orchids, ferns), tank (bromeliads), succulence (cacti)

Lecture 5: Population Ecology – Models Without Age Structure

- Population = collection of individuals
- Population density = N/A (N = # of individuals)
- Notion of individual more ambiguous w/ plants
 - o Ex. aspens → one seed produces many identical connected stems (clones)
 - o Ex. dandelions → many identical seeds produce many identical unconnected plants
 - o Ex. larkspur → many unique seeds produce many unique plants

Population growth models (basic)

	Density independent	Density dependent
Discrete time steps Difference equations Arithmetic	Geometric <i>*add age structure</i>	none
Continuous time steps Differential equations Calculus	Exponential	Logistic <i>*add allee effects, time lags</i>

*Extensions for greater realism

- Population models aim to predict trajectory of population growth through time
- Individuals in population now = N_t
- Individuals in population one step later = N_{t+1}
- General model is $N_{t+1} = f(N_t)$
- Challenge: choosing simple but realistic parameters for f
- Discrete model good for temperate animals (breeding seasons) → time step can be 1 year
- Continuous model good for humans → sex year round

Geometric growth model

- N can change by births /deaths (assume no immigration/emigration)
- Simple model: $N_{t+1} = N_t + B - D$
- If B/D during one time step treated as **per-capita rates** that are **fixed constants**, then:

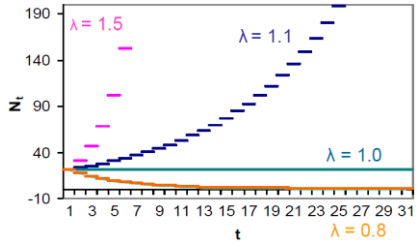
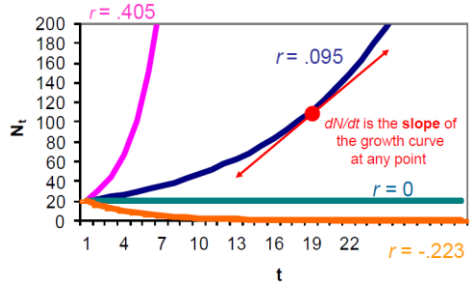
$$N_{t+1} = \lambda N_t$$
- λ = **growth rate constant** (factor by which N changes over 1 unit time)
 - o $\lambda > 1$, births exceed deaths → population ↑
 - o $\lambda < 1$, deaths exceeds births → population ↓
 - o $\lambda = 1$, births = deaths → population constant (unlikely)

Exponential growth model

- To apply model to continuous time, per-capita rates of birth/death are instantaneous
- **Growth rate constant** becomes **r**

$$\frac{dN}{dt} = rN$$
- Similarly,
 - o $r > 1$, population ↑ exponentially
 - o $r < 1$, population ↓ exponentially
 - o $r = 1$, population constant (unlikely)

Geometric vs. exponential models

Geometric	Exponential
$N_{t+1} = \lambda N_t$	$\frac{dN}{dt} = rN$
Solve for N_t vs. t : $N_t = N_0 \lambda^t$	Solve for N_t vs. t : $N_t = N_0 e^{rt}$
 <p>The graph shows four discrete growth curves starting from N=20 at t=1. The blue curve (λ=1.5) increases most rapidly, reaching N=190 at t=31. The green curve (λ=1.1) increases more slowly. The red curve (λ=1.0) is a horizontal line at N=20. The orange curve (λ=0.8) decreases over time, reaching N=-10 at t=31.</p>	 <p>The graph shows four continuous growth curves starting from N=20 at t=1. The purple curve (r=.405) increases most rapidly. The blue curve (r=.095) increases more slowly. The red curve (r=0) is a horizontal line at N=20. The orange curve (r=-.223) decreases over time. A red dot on the blue curve is labeled 'dN/dt is the slope of the growth curve at any point'.</p>

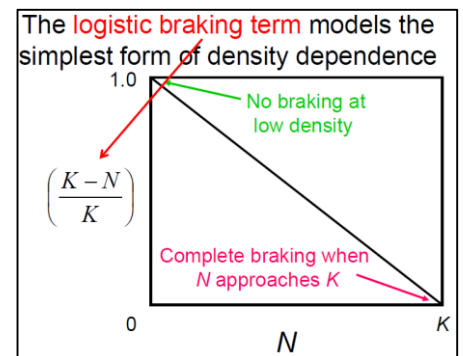
- All species have potential for +ve population growth (λ or $r > 1.0$) under good conditions
- All species have potential for -ve population growth (λ or $r < 1.0$) under bad conditions
- But no species has maintained λ or $r > 1.0$ for long period (similarly, no extinct species has maintained λ or $r < 1.0$ for long period)
- \therefore Mechanism in environment to keep populations from exploding \rightarrow density dependence (growth depends on N)

Logistic growth model

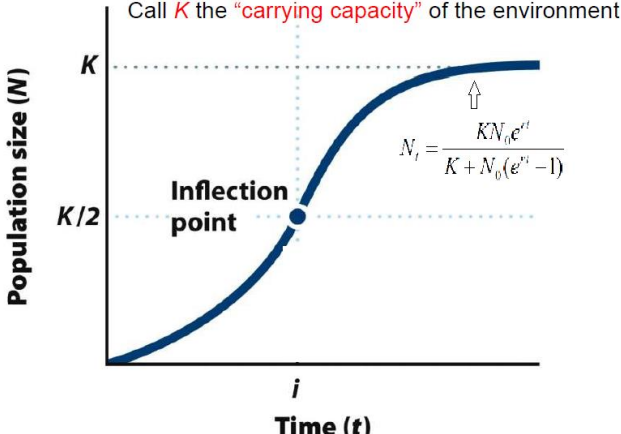
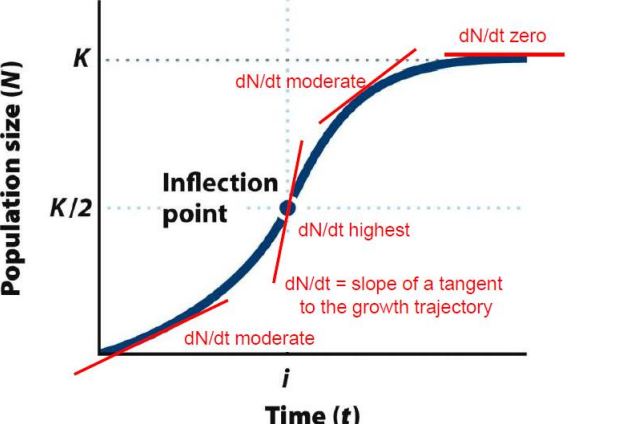
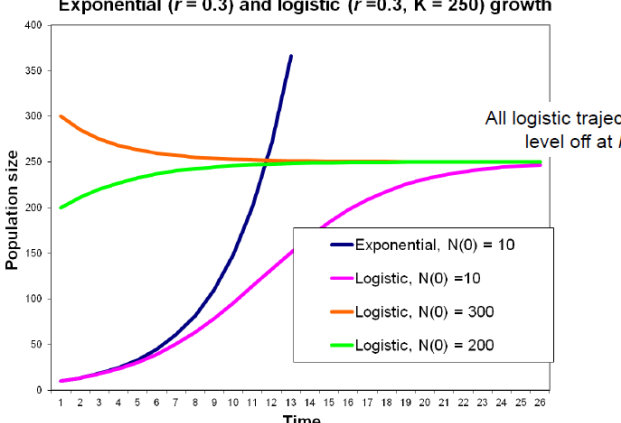
- Factors in **density dependence** with K
- $K =$ **carrying capacity** of environment (rate of resources being used)
- If N is small (less overcrowding, less competition for resources) $\rightarrow (K - N)/K$ is near 1
- If N is big (overcrowding, competition for resources) $\rightarrow (K - N)/K$ much less than 1
- $(K - N)/K =$ **logistic braking term**
- Exponential growth model + new term added for “brakes”

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

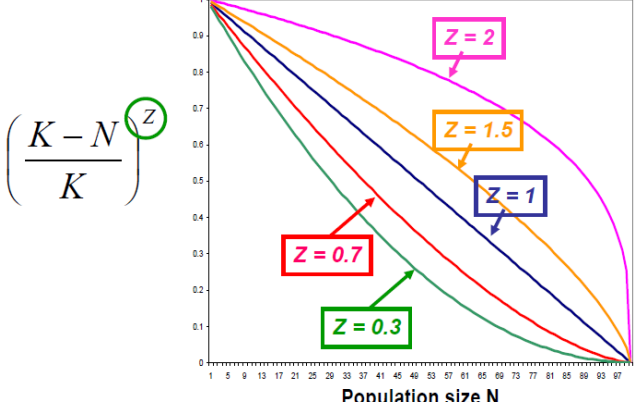
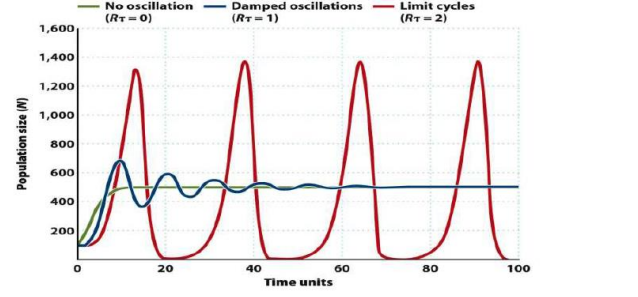
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STOP!



Logistic model in graphical form

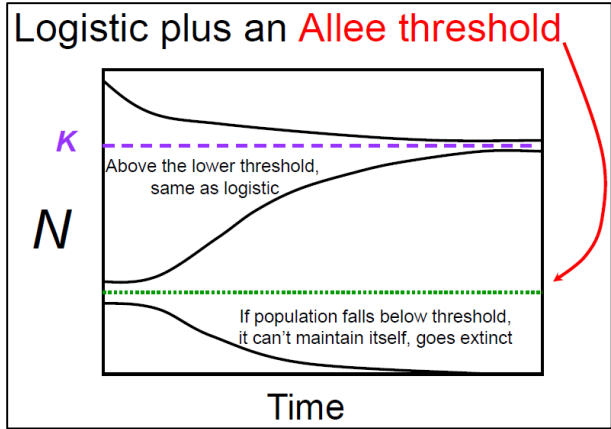
Simple form of density dependence	
<p>Solving logistic model for N_t vs. t gives sigmoid growth curve</p> $N_t = \frac{KN_0 e^{rt}}{K + N_0(e^{rt} - 1)}$ <p>*Don't need to remember</p>	<p>Call K the "carrying capacity" of the environment</p>  <p>Population size (N)</p> <p>Time (t)</p> <p>Inflection point</p> <p>$N_t = \frac{KN_0 e^{rt}}{K + N_0(e^{rt} - 1)}$</p>
<p>Population growth maximized at $N = K/2$</p> <p>When $N \downarrow$ population growth slower b/c less individuals to mate with</p> <p>When $N \uparrow$ population growth slower b/c overcrowding, competition for resources</p> <p>Population growth stops at $N = K$ (when carrying capacity reached)</p>	 <p>Population size (N)</p> <p>Time (t)</p> <p>Inflection point</p> <p>dN/dt highest</p> <p>dN/dt moderate</p> <p>dN/dt moderate</p> <p>dN/dt zero</p> <p>$dN/dt = \text{slope of a tangent to the growth trajectory}$</p>
<p>Note: Logistic trajectories only truly sigmoid when population starts low</p> <p>If population starts above and near K, population declines to K</p> <p>If population starts below and near K, population rises to K</p>	<p>Exponential ($r = 0.3$) and logistic ($r = 0.3, K = 250$) growth</p>  <p>Population size</p> <p>Time</p> <p>All logistic trajectories level off at K</p> <ul style="list-style-type: none"> Exponential, $N(0) = 10$ Logistic, $N(0) = 10$ Logistic, $N(0) = 300$ Logistic, $N(0) = 200$

- Although logistic model better than exponential model (includes density dependence), still too simple \rightarrow specifies one kind of density dependence w/ perfect compensation
- Above logistic model implies all populations gradually and smoothly approach K and maintain equilibrium forever
- In reality, density dependence likely to be non-linear, may overshoot K (see graphs below)

Realistic forms of density dependence	
<p>1. <i>Allow braking function to have different shapes</i></p> <p>Add variable exponent $z \rightarrow$ get whole family of different braking functions</p> <p>$Z=2$ realistic for most populations \rightarrow K does not affect N that much as first, but as $N \uparrow$ K more dramatic (not as gradual)</p>	 <p>The graph shows the braking function $\left(\frac{K-N}{K}\right)^z$ on the y-axis (ranging from 0 to 1) against Population size N on the x-axis (ranging from 0 to 100). Five curves are plotted for different values of z: $z=0.3$ (green), $z=0.7$ (red), $z=1$ (blue), $z=1.5$ (orange), and $z=2$ (magenta). As z increases, the curve becomes steeper as N approaches K.</p>
<p>2. <i>Time delays</i></p> <p>Green curve \rightarrow no time delay</p> <p>Blue curve \rightarrow moderate time delay, population overshoots K (has “momentum” to pass K) but eventually levels off</p> <p>Red curve \rightarrow extreme time delay, curve keeps oscillating and never levels off</p> <p>*In reality, population would probably overshoot then go down to (extinction) as opposed to making recovery to overshoot again</p>	$\frac{dN_t}{dt} = rN_t \left[1 - \frac{N_{t-\tau}}{K} \right]$ <p>Increasing delay (τ) causes increasing overshoots and cycling</p>  <p>The graph shows Population size N on the y-axis (0 to 1,600) versus Time units on the x-axis (0 to 100). Three scenarios are shown: - No oscillation ($R\tau = 0$): A smooth green curve that levels off at $N=500$. - Damped oscillations ($R\tau = 1$): A blue curve that oscillates around $N=500$ before settling. - Limit cycles ($R\tau = 2$): A red curve that oscillates between approximately 0 and 1,400.</p>

Allee effects

- Logistic model implies lower populations always have faster growth rates
- **Allee effects = negative effects of low density**
- These effects arise from **social benefits** (ex. mate finding, group living, group defense)
- \therefore Populations may fluctuate b/w K (upper limit) and another threshold (lower limit)
- Dropping below lower limit \rightarrow extinction
- Very important in wildlife conservation



Lecture 6: Age-Structured Populations and Life Histories

Life history

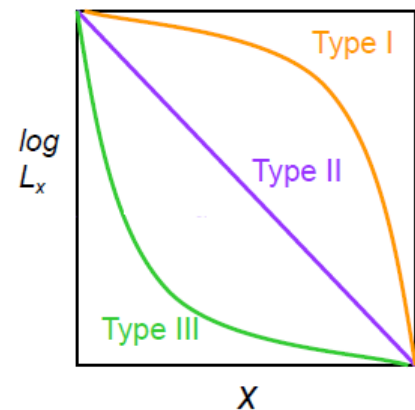
- Fundamental events during life
- *Birth*: start at small size
- *Growth*: no reproduction, **resource accumulation**
- *Sexual maturity*: reproduction (with enough resources) → organisms show various lifestyles

Age-structure populations

- Single population, but considering fecundity and survivorship
- **Survivorship** = chances of survival
- **Fecundity** = capacity to reproduce
- Variations of these summarized by life tables, age-specific rates
- Without age structure, population models assume individuals equal in capacity to contribute to population size change
- With age structure, there are **age classes** (arbitrary time units, depends on species)
- Ex. bacteria age classes minutes/hours, human age classes 5 years

Survivorship

- x = age class
- L_x = probability of being alive at age x
- $L_0 = 1.0$
- Survivorship curve = graph of L_x vs. x
- **Type I**: survivorship ↑ early in life, rapidly dying off near end of life (ex. humans, large mammals)
- **Type II**: constant probability of death (i.e. half life)
- **Type III**: survivorship ↓ early in life, rapidly dying off at beginning of life (ex. plants, insects → produce huge number of offspring)
- Survivorship curve for humans more complex



Fecundity

- b_x = avg # daughters born to female of age x (during time interval x to $x+1$)
- Reproductive period preceded by resource-accumulation
- **Fecundity-survivorship trade-offs** (i.e. cost of reproduction) → if female reproduces heavily, uses up lots of resources = decrease in survivorship

Life tables

- Summarize statistically expected life events for average individual of specific age
- Females only (males do not reproduce ∴ do not contribute to population size change)
- $R_0 = \sum L_x b_x$ = **net reproductive rate**
- Formula works b/c $\sum b_x$ is total # daughters produced by mother who doesn't die early, multiplying by L_x discounts expected production by probability that some mothers die early
- R_0 in time units of one generation

$$T = \frac{\sum x L_x b_x}{\sum L_x b_x} = \frac{\sum x L_x b_x}{R_0} = \text{generation time} = \text{average age female gives birth}$$

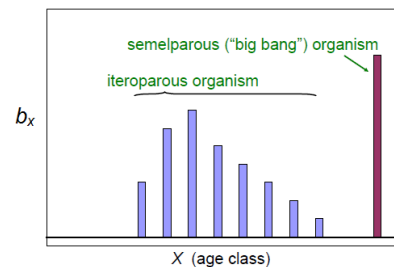
- R_0 and λ similar \rightarrow population growth rates; but R_0 in generations (w/ age structure) and λ in time steps (w/o age structure)
- $R_0 = \lambda^T$ and $\lambda = R_0^{1/T}$

Constraints/trade-offs of reproduction

- Generally: $\uparrow R_0$ or $\lambda = \uparrow$ reproduction = \uparrow fitness
- So why isn't there selection for higher growth rates? (Why aren't all plants annuals? Why aren't all lives short and fast?)
- Longer reproductive periods = \uparrow resource accumulation
- If reproduce too early, not enough resources
- **Fecundity-survivorship trade-offs**
- Ex. glacier lily study \rightarrow plants that produce \uparrow fruit (i.e. \uparrow reproduction) have \downarrow corm growth b/c using resources to reproduce

Life history alternatives

- **Iteroparous**: repeated reproduction of less offspring, multiple age classes reproduce
- **Semelparous**: single reproduction of hundreds of offspring at once then die, spend long periods accumulating resources
- Semelparous plants = "monocarpic"
- Ex. basal rosette ("century plant") \rightarrow grows for decades then triggering event to produce tree-sized flower stalk, dies after
- Ex. salmon \rightarrow semelparous animal



Plant life histories

Seasons of growth	Semelparous	Iteroparous
1	annual	—
2	biennial	—
More than 2	monocarpic perennial	perennial

Reasons for semelparity

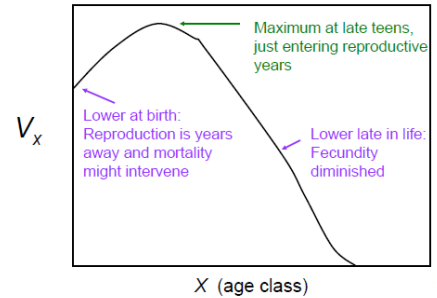
- Annual/biennial semelparity explained by **seasonality**
- Many year semelparity explained by \uparrow resource accumulation over longer period leading to \uparrow reproductive output
 - o **Size dependent mating success**: pollinators/seed dispersers attracted to massive flower/fruit displays (bigger size) $\rightarrow \therefore \uparrow$ pollinator preference to provide resources
 - o **Predator satiation**: predators eat seeds, bigger size can produce massive seed crops $\rightarrow \therefore$ satiation of seed predators, allowing more seeds to go uneaten
- Semelparity expected to evolve when adult survival low

Local synchrony: result of semelparity

- Reproduction of species all at once
- Advantageous for pollination b/c \uparrow # seeds = **predator satiation tactic** (ex. of Allee effect)
- Ex. monument plant \rightarrow semelparous and local synchrony
- Ex. bamboo \rightarrow semelparous and extreme synchrony (even across world they bloom at once)
- Ex. blue oak \rightarrow iteroparous and local synchrony ("masting")

Reproductive value (extension of life tables)

- v_x = reproductive value = expected # future daughters left to individual of age x
- v_x ↓ early and late in life, v_x ↑ in late teens
- Important for **conservation** → when to release animals in captive breeding/release programs or when to introduce animals to new habitats (dispersal), should coincide w/ age of high v_x
- Important for how selection acts on behaviour → ↑ v_x = ↑ **mate attraction**



Antagonistic pleiotropy

- **Pleiotropy**: one gene may have multiple diff functions
- **Antagonistic pleiotropy**: a gene may have opposite effects on survival at diff ages
- Gene w/ **positive** value in **young** animals but **negative** value in **old** animals favoured by natural selection
- Why? Natural selection selects for ↑ fitness = reproducing early
- Ex. protein p53 is stem cell reducer → suppresses tumours when young but causes premature aging by destroying stem cells later
- Antagonistic pleiotropy predicts many such genes will accumulate = **senescence**
- ∴ No cure for aging b/c natural selection will continue to choose for a bunch of these genes (“Darwinian medicine”)

Dispersal

- Movement of individual(s) away from population born in
- Organisms disperse b/c of climate change, avoidance of inbreeding
- Costs of dispersal include ↑ energy expenditure, unfamiliar habitat, predation
- Dispersal influences genetic drift
- Limits to dispersal include physical barriers (ex. mountains), physiological constraints (ex. temp ranges), anthropogenic barriers (human made, ex. roads, farming)

Active dispersal

- Changing location by organism through own ability, usually **density dependent** (resource competition, habitat quality/size, social structure)
- Ex. populations that rely on one adult male to reproduce force juvenile males to disperse
- Flying/aquatic animals usually more mobile than terrestrial

Passive dispersal

- Immobile plants/animals rely on **dispersal** units to aid in reproduction or exploitation of new habitats
- Dispersal units adapted for movement by specific environmental dispersal agents (wind, water, other animals, motile larvae stage)
- Ex. sponges, corals → release gametes into water
- Ex. plants → seeds, fruits have wings/hairs to be carried by winds; sticky to catch onto mobile animals; dispersed in feces of animals that feed on them

Lecture 7: Species Interactions – From 2-Species Population Models to Community Structure

Species interactions

- Classified by who benefits (+) and who suffers (-)
- **Consumer-resource** (+/-)
 - o Predator-prey
 - o Herbivore-plant
 - o Parasite-host
- **Competition** (-/-)
- Mutualism (+/+)

LV model of intraspecific competition

- Coevolution: when 2 species affect each other's evolutionary trajectory
- Logistic model → only *intraspecific* competition (one braking term)
- **Lotka-Volterra model** → *intraspecific* and *interspecific* competition (add second braking term to logistic)

Recall logistic model: $\frac{dN}{dt} = rN \left(\frac{K-N}{K} \right)$

Given two species, LV model for species 1:

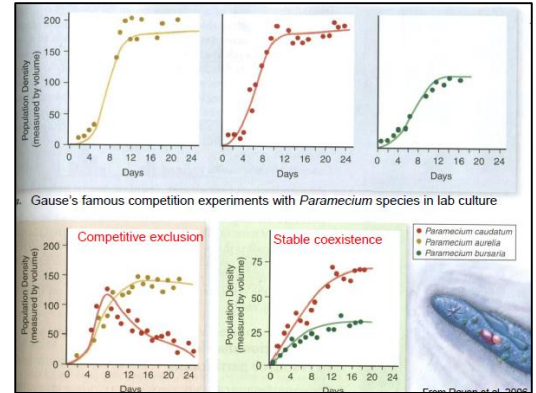
$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right)$$

- Reverse coefficients to write equation for species 2
- Equation can be expanded to consider n species
- $\alpha_{12} N_2 =$ **competition coefficient** (braking term for sp 2, i.e. effect on sp 1 by sp 2)
 - o If $\alpha = 0$, no competition b/w species
 - o If $\alpha = 1$, species using resources at same rate
 - o If $\alpha < 1$, low competition
 - o If $\alpha > 1$, high competition
- Equilibrium b/w species depends on K and α
 - o Both species may stably **coexist** → requires **both species to inhibit their own growth more** (density dependent) than they inhibit each other
 - o Sp 1 may win ($N_1 = K_1, N_2 = 0$)
 - o Sp 2 may win ($N_2 = K_2, N_1 = 0$)
 - o Winner depends on N → sp that starts w/ N near K will usually win

Law of competitive exclusion

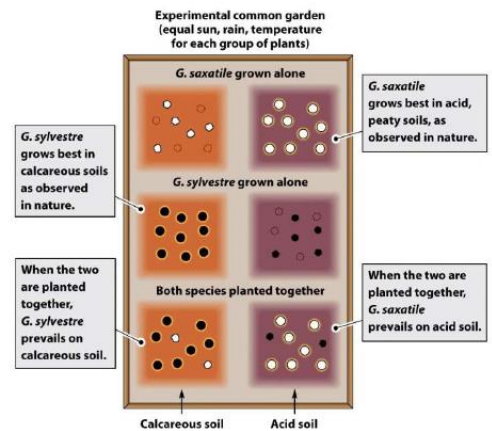
- LV models produce unstable outcomes → complete competitive exclusion
- **Complete competitors cannot coexist**
- I.e. if α very high, other species driven to extinction
- Realistically, not true b/c habitat complexity (other species)

- **Ex. Gause's protozoa experiments:**
 - o Top graphs: species by themselves (they approach K)
 - o Bottom 1st graph: red sp outcompeted by yellow sp, red sp driven to extinction (yellow sp better at obtaining resources)
 - o Bottom 2nd graph: red and green sp can coexist (although they are still using same resources as their K for bottom graph less than K's in top individual graphs)
 - o *Experiments done in controlled lab environment (no habitat complexity)



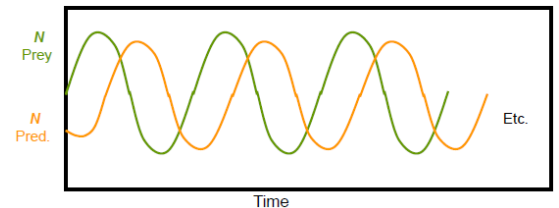
Realistic competition in nature

- **Complete competitive exclusion not likely**
- Natural selection selects for **higher competitive ability** or for **reducing resource-use overlap**
- **Ex. Galium bacteria experiment:**
 - o Black sp wins on orange (basic) soil
 - o White sp wins on purple (acidic) soil
 - o In real life, both sp can coexist b/c soil not completely basic/acidic (∴ reduce overlap)
- **Ex. Intertidal species study:**
 - o Species must be adapted to both tides, but also compete for space
 - o Upper limits: receding tides cause abiotic stress (some sp cannot physically survive)
 - o Lower limits: no receding tides cause biotic stress (competition for space here)



Predator-prey cycles

- LV model predicts cyclic populations for predators/preys, too simplistic though
- Hard to replicate in lab, often predator will consume all prey ($N_{\text{prey}} = 0$) and starve ($N_{\text{predator}} = 0$)
- **Ex. Huffaker experiment on prey/predator mites:**
 - o Able to reproduce cycle by complicating space (i.e. allowing prey refuge on oranges), only lasted 3 cycles
- **Ex. Real life lynx-hare cycle:**
 - o Predator-prey cycle unusual in real life
 - o Arctic is relatively simplistic environment (not many species)
 - o Lynx-hare cycle not just simple LV model, but LV does play part
 - o Additional factors → hare-plant cycle (heavy browsing degrades quality of plant food available for hares), social stresses in overcrowded hare populations (endocrine collapse)



Niche theory (extension of LV model)

- If assume that competitive exclusion is driving force, then **coexistence requires differentiation**
- Differentiation measured by specie's ecological **niche** → describes role in resource use
- Niche overlap (resource overlap) can represent competition coefficient α

- Ex. if no overlap, then $\alpha \approx 0$
- Ex. if \uparrow overlap, then $\alpha \approx$ very high
- **Niche theory**: community composition determined by features that allow coexistence
 1. **Limiting similarity**: niches should be sufficiently different to allow coexistence
 2. **Resource partitioning**: expect to see similar organisms dividing up resources
 3. **Assembly rules**: some species pairs incompatible, i.e. if sp A established in area first then sp B cannot establish
 4. **Character displacement**: coexisting similar species should evolve differences
- **Ex. Warbler bird study on resource partitioning**:
 - Up to 20 different warbler species in one forest $\rightarrow \alpha$ should be high, but coexist
 - Can coexist b/c feeding from diff parts of tree = “resource partitioning”
- Above theory only applicable if little abiotic factors
- However, b/c there *are* harsh environmental factors, niche theory died out b/c too simple

Realistic community structure

- Most communities not competitive equilibrium
- Real populations kept **below carrying capacity** by weather, disease, predation
- Conditions fluctuate, favouring diff sp at diff times
- **Ex. Starfish predation study**:
 - Mussels able to outcompete other sp for space
 - Starfish prey on mussels
 - When starfish removed from some areas, mussels pushed out other sp = \downarrow biodiversity
 - \therefore Predation can reverse competitive dominant species
- Explains why many species do not reach super high N \rightarrow **predation controls N**
- Also, most sp not isolated populations, rather **metapopulations** connected by dispersal
- Ability of organisms to move b/w diff populations prevents competitive exclusion
- Ex. sp A and sp B:
 - If A outcompeted by B in habitat patch \rightarrow local coexistence impossible
 - However global coexistence possible if: A must sometimes go extinct in patch or new patches must be created from time to time; or B must be better disperser than A
- \therefore **Metapopulations stabilize competition** \rightarrow allow for prey-predator coexistence
- **Coexistence possible b/c diff life histories** (not diff resource-use niches)

K vs. r strategy

<i>K strategy</i>	<i>r strategy</i>
- Slower growth	- Faster growth
- Longer generation time	- Shorter generation time
- Larger body size	- Smaller body size
- More investment in somatic growth	- More investment in gonad growth
- Lower reproductive rate	- Higher reproductive rate
- Good competitors	- Poor competitors
- Poor at dispersal	- Good at dispersal
- More investment in offspring (ex. heavier seeds)	- Produce more but lighter seeds
- Iteroparity more likely	- Semelparity more likely
- Shade tolerant (plants)	- Shade intolerant; seed dormancy
	- Born to run

Lecture 8: Metapopulations, Plant Community Composition

Metapopulations: example blue butterfly population persistence

- In Oregon 1850 a valley was all native prairie abundant w/ lupine, now only 0.5% left (agriculture)
- Butterfly discovered 1920, thought extinct by 1931, rediscovered 1989 on brink of extinction
- Butterfly now known from 13 small prairie fragments
- Life history: annual cycles of reproduction then random dispersal across habitat
- Caterpillar stage can only eat a rare plant species (lupine) → heavy larval mortality → females must find prairie patches w/ lupine
- **Ecobaker model**: explicit spatial map of butterfly population persistence
- For butterfly model, many different patches of butterflies but only ones w/ biggest patches (more resources) stay alive
- Butterflies can **disperse** to new patches and **repopulate** a patch that went extinct
- They cannot survive solely on resources of small patch (not enough) but can survive if there is nearby patch w/ reservoir of resources

Metapopulations: example pika population persistence

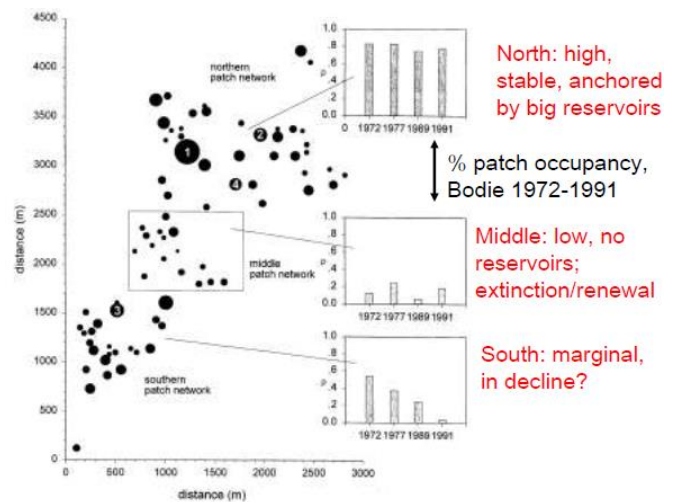
- Old mining town in California → tailing piles from hard-rock mining created many small replicated patches of pika habitat
- Research divided patches into north, middle and south

1. North zone

- o High, stable populations
- o Anchored by **big reservoirs** of resources
- o Especially patches 1, 2, 4 (always had pika in them)
- o Pika able to move from these patches (1, 2, 4) and disperse between other patches
- o **Source** patch for middle zone

2. Middle zone

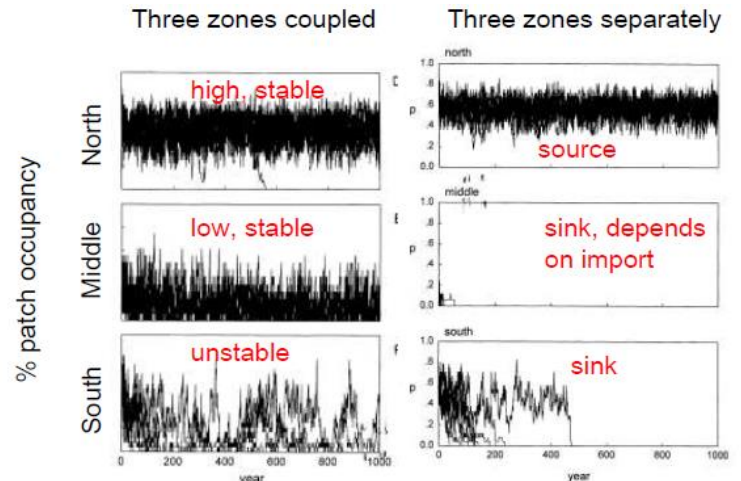
- o Low, stable populations



- No reservoirs
- Extinction/renewal → pikas from north zone can repopulate when middle zone extinct
- **Sink, depends on import**

3. South zone

- Unstable population, decline
- Often extinct
- **Sink**



Conclusions: stability and coexistence

- *Model* populations can be driven to extinction in several ways:
 - **Strong density-dependence** (overshoot and crash)
 - **Unstable competition**
 - **Unstable predator-prey** (also disease-host)
 - **Allee effects at low density**
- But these tendencies are *countered* by:
 - **Non-equilibrial conditions**
 - **Habitat patchiness**
 - **Rescue by migration**
 - **Variation in life history strategy**

Plant community ecology

- Community types → what sets of species regularly occur w/ each other?
- Examples of significant species associations: beech-maple forest, oak-hickory forest, bur-oak savannah
- Two theories: organismal and individualistic

Clements: organismal

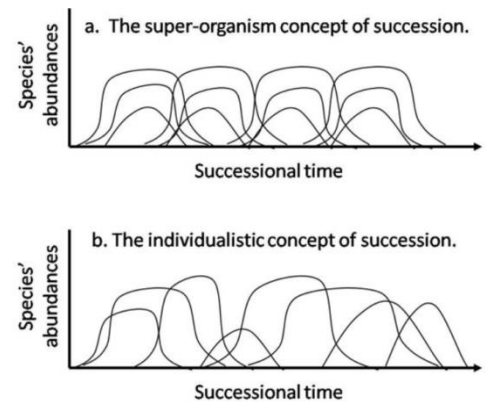
- Species distributed dependently of each other (depend on each other specie's presence)
- Certain species found together b/c **biologically integrated**
- Typological community concept → “types” of communities w/ distinguishing species
- Species are one “**super organism**”
- I.e. distribution based on biotic factors

Gleason: individualistic

- Species distributed **independently** of each other
- Certain species found together b/c similar abiotic tolerances
- Why species are found where they are limited by:
 1. **Dispersal**
 2. **Filtering** (by physical environment, ranges of tolerance)
- I.e. distribution based on abiotic factors

Testing the theories

- At first Clement's theory accepted
- But decades later, using gradient analysis data Gleason's theory proved correct
- **Whittaker**: direct gradient analysis of Arizona mountains, sample plant occurrences at many points through ranges and plot along environmental gradient (elevation or moisture)
- Graph a: organismal theory – species should all grow and die at same time (as one organism)
- Graph b: individualistic theory – species grow and die at own time
- **Data conformed to graph b**
- **Curtis**: indirect gradient analysis, same result
- Margaret **Davis**: used pollen data to track path and timing of tree species as glaciers retreated
→ different tree species migrated at different times and paths ∴ tree communities didn't migrate as units, membership varied continuously (i.e. individualistic, not organismal)
- **Modern consensus for terrestrial vegetation distribution:**
 - **Primarily individualistic**, strongest environmental filtering driven by physical factors
 - However, some species interactions (ex. herbivory) **secondarily** affect distribution
- Note animal communities much less individualistic than plant communities (can remove one species and completely change community)



Lecture 9: Spatial Ecology, Plant Communities and Disturbance

Plant successional change

- Plant species colonize in predictable way
- **Successional change**: one species dominates for a while, then new species comes in and replaces them
- Vegetation changes spontaneously as vegetation itself modifies environment (not driven by anything specific, it just happens)
- Classic successional sequence:
 - o First species to appear called **pioneer species** (from dispersal or seed bank in soil) → r-strategists or “weedy,” typically short-lived annuals, good at dispersing, make lots of seeds
 - o Goes through temporary, non-equilibrium stages (**different species adapted to different conditions** throughout succession coming in/dropping out)
 - o Ends at stable **climax stage** with set of species adapted to conditions, keep replacing themselves (no more change) → K-strategists, big plants, good competitors, likely to be shade-tolerant, don’t make many seeds
- **Primary succession**: new substrate created, no pre-existing vegetation (ex. sand dunes, retreating glaciers)
- For primary succession, development of more complex soil most important b/c more nutrient rich soil lets more plants grow
- **Secondary succession**: pre-existing vegetation undergoes **disturbance**
- Disturbance: discrete event that causes abrupt change in ecosystem, community, population; sets back succession (ex. fire, windstorm, logging, agriculture)
- Secondary succession much more common

Primary succession example: lava flows in Hawaii

- **Stage 1**: After lava flow, very harsh environment → tough pioneer plants can establish (**seeds** and **spores** that blow in)
- **Stage 2**: Soil lava erodes into finer particles, dead plants contribute to organic matter → development of **more complex soil**, more plants can establish in better soil
- **Stage 3**: Animals aid in introduction of new species by consuming and dispersing seeds
- **Stage 4**: 20-30 years later: herbaceous plants cover ground, trees grow (no bare soil left)
- **Stage 5**: 100 years later: **forests** with substantial canopy (shade becomes important), soil well developed

Secondary succession example: old field

- Usually studied in **old-field** environments → abandoned farms, agricultural land left to go back to nature
- **Stage 1**: After abandonment by farmer, first stage is big flush of **annual weeds** → weed seeds usually require a lot of sunlight to germinate, b/c farmer plowed land before seeds now exposed to sunlight w/ no crops left and can germinate (also need very wet season to trigger)
- **Stage 2**: **Perennial weeds** for several years
- **Stage 3**: **Woody shrubs** move in, small trees
- **Stage 4**: **Colonization by trees**, tree saplings

- **Stage 5:** Colonization continues, **forest canopy** closes in → shade becomes main factor
- **Stage 6:** Shrub layer thins, **shade-tolerant understory only** (they can photosynthesize w/ low levels of light, also photosynthesize in winter right before blooming of taller trees)
- **Stage 7: Climax community** → only canopy tree species and shade-tolerant species remain, forest perpetuates itself to **steady state**, species turnover minimal

Drivers of terrestrial succession

- **Soil development:** plant species dies and become organic matter, provides better soil for future plants to grow → especially important in primary succession
- Includes accumulation of organic matter, N content, pH buffering, water retaining capacity
- **Shading:** shade-tolerant species replace shade-intolerant species → especially important in secondary succession
- Mechanisms involved in succession:
 - **Facilitation:** early successional species modify the disturbed environment, making it more hospitable to later successional species
 - **Inhibition:** earlier successional species dominate the environment inhibiting colonization of later successional species until the area is again disturbed
 - **Tolerance:** early successional species grow and reproduce quickly, and are eventually replaced by slower growing species that reproduce later

Succession where no climax equilibrium reached

- Ideally succession reaches stable climax configuration of dark shade, organic-rich soils
- However, succession not always stable:
 - **Climax species cannot replace itself** → ex. in boreal forests, successional changes lead to spruce-fir forest but does not replace itself (no spruce-fir seeds under tree, so in event of disturbance spruce-firs do not regenerate, succession starts over)
 - **Acid, sandy soils** → pine-oak leaf litter makes soil more acidic, not richer
 - **Fire-prone ecosystems**
 - Systems driven by **seasonality**, ex. plankton in temperate lakes
 - **Cycling of dominants** (A replaces B, then B replaces A)
 - **Transient substrates**, ex. decay of log (does not lead to climax, ends up in disappearance of log)

Rainforests succession

- Rainforest very unlikely to burn (not dry enough)
- Undergoes **gap-phase succession**
- When large tree falls, creates canopy gap → pioneer species able to come in again (vegetative turnover)
- Canopy trees connected by “Tarzan ropes” so when one tree falls, takes down others too
- Pioneer species found in these gaps all over rainforest

Fire-dominated communities

- Habitats that tend to **build up flammable fuel** overtime
- Ex. Pine forest → pine leaves produce flammable chemical that evaporates into air when hot/dry, also pine needle litter (thick layers on ground if no recent fire) adds to fuel
- Ex. Australian Eucalyptus trees → leaves produce flammable essential oils

- Ex. Mediterranean climate of Chaparral → sclerophyll leaves have very flammable compounds
- **Ground fire**: bigger trees have thicker bark, also SA/V advantage of being large helps them survive (small trees die)
- **Crown fire**: if enough fuel and enough branches on bottom of trees, ground fire can jump to crown fire; also gust of wind can ignite by bringing oxygen to very hot/flammable air surrounding trees

Adaptations to fire: serotinous pine cone example

- Pine cones have scales which open up to release seeds (seeds are samaras w/ papery wings for wind dispersal)
- Scales held together by resin
- When fire, resin separates and cone starts open → releases seeds hours after burning
- Advantageous b/c fire will wipe out vegetation ∴ no competition for seeds
- This adaptation in plants called **serotiny**
- Other adaptations include: germination or flowering triggered by heat/smoke, opening of hard shells by heat shock (liberates seeds or allows water to enter), and fertilization of soil (purging of toxins) by smoke

Ecobeaker model: fire

- Map of habitat = checkerboard w/ many sites or cells
- Each cell occupied by one species of plant
- From one time interval to next, each cell can change its state from one species to another
- Changes occur according by chance, according to specified transition probabilities (**stochasticity**)
- Ex. if probability of change from oak to maple = 0.2, then randomly chosen 20% of cells that are now oak will change to maple at next time interval
- Without fire, one species eventually dominates all others (biodiversity = 1)
- Adding fire spreads and empties cells → controls dominating species, allows for secondary succession to start in patches (biodiversity ↑)
- In model, we can see different patches at different stages of succession b/c different times of disturbance

Conclusion: Spatial ecology

- “Climax” terminology in disuse, now “**old-growth**”
- Regions and ecosystems have **characteristic disturbance regimes** → most “equilibriums” are quasi-equilibriums at most
- Spatial scale matters → gap-phase succession
- Habitats are mosaics of **patches in different stages of regrowth** after disturbance
- **Intermediate disturbance hypothesis** for maximum species diversity
- More than a static picture (i.e. species reaching carrying capacity or equilibrium) → about ways environment poses challenges to species and how environment changes over time

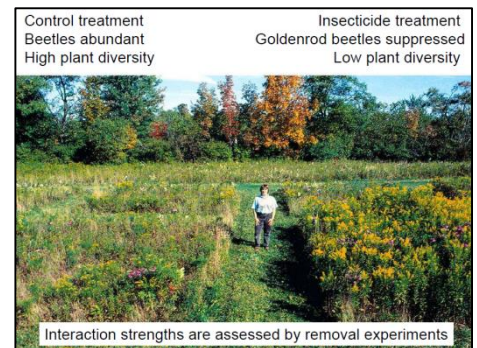
Lecture 10: Trophic Relationships in Communities

Trophic levels

- Primary producers = plants
- Primary consumers = herbivores
- Secondary consumers = carnivores who eat herbivores
- Tertiary consumers = carnivores who eat secondary consumers
- Detritivores = eat dead organic matter

Trophic relationships

- Food chains/webs → network of species connected
- However, food webs cannot tell us strength of interaction b/w species → more important is experiments (especially **removal experiments**)
- Classic experiment is starfish removal study (from lecture 7)
- Another example: insecticide treatment study
 - o Insecticide treatment = ↓ goldenrod beetles = ↑ goldenrod plants (good competitors) = ↓ biodiversity
 - o No insecticide treatment = ↑ goldenrod beetles = ↓ goldenrod plants = ↑ biodiversity



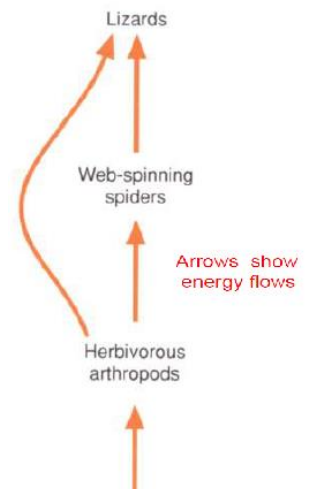
Trophic cascades

- Famous **HSS paper**
- Food supply for herbivores is limited (not infinite amount of plants) → herbivores should grow to population size where eat all vegetation (resources)
- However, b/c **“the world is green”** i.e. all the vegetation is not gone, there must be other limiting factor for herbivores = **carnivores**
- Herbivores eating plants = direct negative effect on plants
- Carnivores eating herbivores = **indirect** positive effect on plants (keep herbivores ↓ so don't limit plant growth)

- **Trophic cascade** = indirect effects that alternate across trophic levels
- Can dramatically affect communities

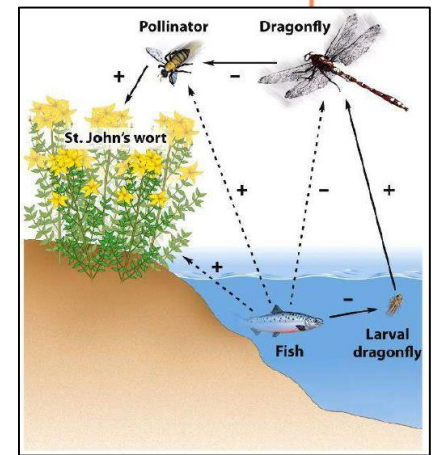
Trophic cascades example: removal of Anolis lizard in Caribbean islands

- Lizard eats spiders and beetles, spiders eat beetles, beetles eat plants
- **Result of removing lizard not clear** : will benefit or harm plants?
- Trophic cascade likely, but cannot answer from food web alone → must experiment by removing lizard
- One hypothesis: ↓ lizard = ↑ spider = ↓ beetles = ↑ plants (benefit plants)
- Another hypothesis: ↓ lizard = ↓ spider = ↑ beetles = ↓ plants (harm plants)
- **Answer after experiments**: lizards do benefit plants
 - o Effect of lizards on spiders weak (i.e. lizards don't focus on eating spiders)
 - o Effect of lizards on beetles strong
 - o ∴ Lizards reinforce, rather than counteract, effect of spiders on beetles
 - o But it could of gone other way → must experiment



Trophic cascades example: effect of fish on plants

- From diagram: solid line = direct effect, dashed line = indirect effect, +/- indicates type of relationship
- Experiments show that ↑ fish = ↑ pollination of plants and ↓ fish = ↓ pollination of plants
- Why? ↑ fish = ↓ dragonfly larvae = ↓ dragonfly = ↑ pollinators = ↑ plants



Interaction b/w trophic levels summary

- Direct and indirect effects can be opposed
- Indirect effects can be as strong as direct effects
- **Keystone consumers** can shift communities b/w alternate states
- Outcomes not fundamentally predictable → **depend on interaction strengths**
- Experiments needed

Plant-herbivore relationships

- Easy to be carnivore: animal tissues easy to convert into animal tissues
- Difficult to be herbivore: plant tissues hard to convert into animal tissues
 - o Cellulose and lignin tough, indigestible w/o microbial symbionts → herbivores usually have whole suite of microorganism to break down **tough fibres**
 - o Plant tissues **heavily defended** against herbivores, chemically and mechanically
- *Note: not all plant tissues difficult to eat/low in nutrition, exception is seeds/fruits (usually sweet to attract animals to eat and disperse seeds)
- Ex. apple sweet but core/seeds very bitter to discourage animals from chewing seeds → seeds go through digestive system of animals and dispersed somewhere else

Chemical defense by plants

- Chemical defense very common (we think plants taste ok b/c food crops artificially selected for low toxicity)
- Plants have many types of **secondary chemicals** called **alkaloids** → do not participate in main functions (photosynthesis/respiration) but are adaptations for defense

- Common alkaloids derived from plants include: caffeine, nicotine, cocaine, dopamine (over 10,000 different ones)
- Causes **coevolutionary race** b/w plants and herbivores
- Responsible for **specialization** and much of biodiversity
 - o Ex. mutation in plant population causes nasty chemical in plant → deters eating by herbivores → plant w/ mutation repopulates
 - o Ex. subsequently, herbivore develops mutation allowing it to eat chemical → ↑ resources for herbivore → herbivore w/ mutation repopulates
- Chemicals often deter generalist herbivores, but no plant species toxic enough to escape **specialist** herbivores (no known plant species in world w/o herbivore)
- Specialist insects can evolve to use chemicals as:
 1. Feeding stimulants
 2. Defense compounds for themselves
- ∴ Herbivore adapted to chemical defense by specialization

Chemical defense: example milkweeds and monarchs

- Milkweeds exude distasteful, poisonous white sap if damaged
- This repellent latex under pressure in leaf veins → insect deterred not only by distasteful sap but also doesn't want to be sprayed by **pressurized sap** by biting into leaf
- Monarch butterfly larva specialized to eat milkweeds → **cuts leaf midrib** to reduce sap pressure before eating and **concentrates cardiac glycosides** (poison) in cuticle to make themselves poisonous and distasteful (deters predators)
- Also, adult monarch and other brightly coloured insects frequently toxic → toxicity signaled by **“warning” coloration** to predators

Mechanical defense by plants

- Graminoids (grasses and similar plants) defended mechanically w/ **silica** in leaves → not poisonous but abrasive (grinds down teeth of animals)
- Also **buds** (growing points of plants) located below soil surface → when animal bites off top of plant, plant not completely killed

Adaptations to mechanical defenses

- Grazing animals (cow, sheep, deer) not as specialized as insects → eat many more and many different plants (more generalized)
- Eat mostly grasses and some **forbs** (plants that aren't grasses that do have alkaloids)
- Adaptation to forbs: dilution or avoidance
- Adaptation to grasses: **fermentation chambers** in gut where microorganisms detoxify and break down tough fibres
- Cattles: fermenting chamber in **rumen** (foregut)
- Horses: fermenting chamber in **cecum** (hindgut)
- Also **specialized teeth** to resist wear of grasses → alternating of tough/weak material to act as file to grind food (grinding food ↑SA/V = better for digestive enzymes to break down)
- Arms race b/w plants-herbivores evident in evolution of herbivore teeth (dinosaur herbivores had smooth teeth)

Chemical defense: problem for ranchers

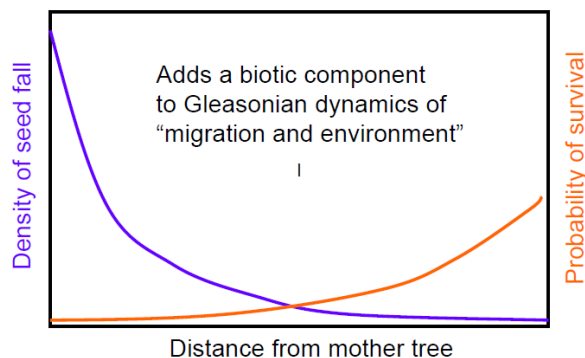
- Grazing animals eat mostly grasses, but also flowers occasionally
- One flower w/ alkaloid that can kill adult cattle/cause miscarriage → seasonality of plant determines when rancher can take cattle up mountains
- Another plant **veratrum** causes deformities in animals (recall mutated baby sheep)
- Veratrum of particular interest in cancer research b/c disrupts developmental pathways

Chemical defense: problem for small mammals (example pika)

- Pikas collect food during summer and store for winter
- Study found pika have different diets for summer/winter
- **Summer**: eat mostly **non-toxic plants** (graminoids, *Trifolium parryi*)
- **Winter**: eat mostly **toxic plant** (*Acomastylis rossii*) collected in summer
- Eat *Trifolium* immediately b/c decomposes quickly in storage (attracts fungi/microbe) and not practical to forage for in winter (too far, risk of predation)
- Hay-piles *Acomastylis* b/c toxins act as preservative to retain food value (deters fungi/microbes), but toxins break down over months in storage

Rainforest diversity

- Biodiversity in rainforests phenomenal
- **Janzen-Connell hypothesis**: partly due to unremitting attack from specialist insects/fungi
- Seedlings have low chance of survival if dropped near mother plant b/c surrounded by species specialized to eat it
- Also no harsh winters to kill off insects/fungi
- Graph: seeds who far further = ↑ chances of survival
- ∴ **Strong density-dependence** prevents species from monopolizing habitat
- Natural selection favours dispersal



Conclusion: Species relationships

- Interactions b/w species and physical environment can produce wonderful adaptations of morphology, physiology and behaviour
- However physical environment is not complex enough to produce extraordinary biodiversity
- Interactions w/ other organism can produce unlimited diversification

Lecture 11: Putting Things Together – Species Interactions in Subalpine Meadows



*Case study: species distribution and abundance in sub-alpine meadow
Why does landscape look this way? (Why are aspen trees interspersed?)*

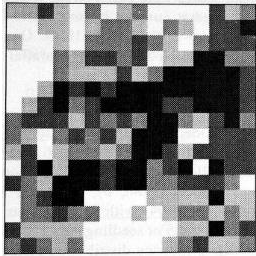
Glacier lily

- Begin w/ looking at one species → glacier lily
- Observe that glacier lilies **abundant where soil surface very rocky** – why?
- **Experiment 1: seed dispersal**
 - o Used adhesive film to trap seeds, measure distance from plant
 - o Found minimal primary dispersal distance (about 20 cm)
 - o Also, no secondary dispersal by ants b/c lack of **elaiosomes** (seeds w/ nutritious chemicals for ants, ants bring back to nest to eat ∴ achieving dispersal)
- **Experiment 2: seed germination**
 - o Treatment 1: buried, organic soil → seeds lasted longest
 - o Treatment 2: exposed, organic soil
 - o Treatment 3: buried, gravel soil
 - o Treatment 4: exposed, gravel soil
- Life history of plant:
 - o Long-lived, iteroparous → grows as “vegetative” plant for years before flowering
 - o Resource storage organ is underground corm
 - o **Seed dispersal distance minimal**
 - o Seeds subject to **desiccation unless in moist conditions**
- **Experiments suggest distribution of glacier lily should be:**
 1. Away from thin soil around rock outcrops (**desiccation**) → observe opposite
 2. Most seedlings near flowering plants (**weak dispersal**) → need to test this
- Next step to gather quantitative data on plant abundance and environmental factors

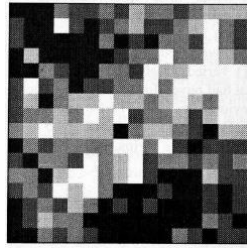
Quantitative tests on plant distribution

1. Flowering plants (count)
2. Vegetative plants (count)
3. Seedlings (subsample)
4. Rockiness (poke rod into ground thousands of times and measure height at which rod stops)
5. Soil moisture (gardening device)
6. Predation risk (soil trails from underground digging)

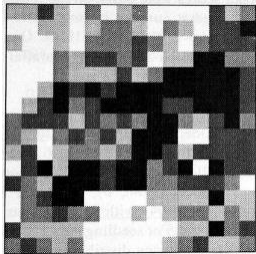
Data heat maps of quantitative test



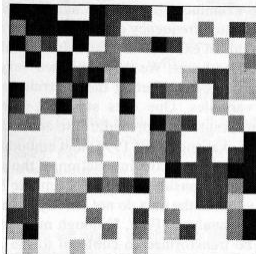
No. flowers



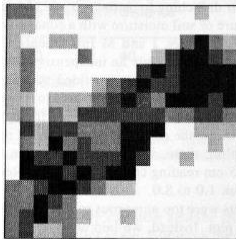
Gopher activity



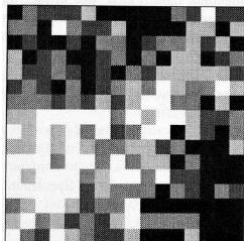
No. vegetative plants



Seedlings



Rockiness



Soil moisture

- Flower and vegetative plant distribution same → expected (means they grow in same place)
- Flower and seedling distribution opposite → not expected b/c low dispersal means seeds should be close to flower
- Flower and rock distribution same → expected (as observed)
- Rock and moisture distribution opposite → expected
- Rock and gopher distribution opposite → expected (gophers avoid rock)

Scattergram matrix

- Shows pairwise correlations b/w variables
- Ovals show trends
- Flowers and rock have positive relationship
- Rock and gophers have negative relationship
- No relationship b/w seeds and other variables

Conclusion from data

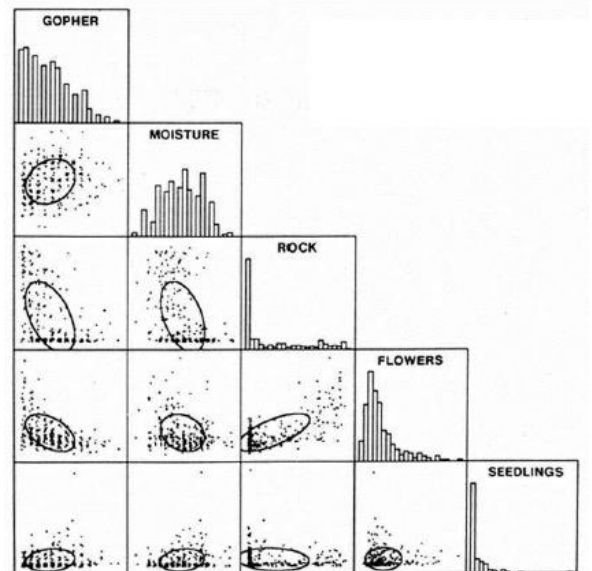
- **“Rock refuge hypothesis”**
- Most seeds produced in rocky areas and fall there, but most desiccate and die
- The few seeds that reach moist, deep-soil areas more likely to survive and produce seedlings
- But seedlings that get established in deep-soil areas likely to be killed by gophers before they reach flowering age (remember long accumulation phase)
- ∴ **Even though rocky habitat physically stressful (b/c desiccation), best for glacier lilies b/c no gophers = ↑ chance of seed survival = ↑ chance of germination = ↑ fitness**

Elements from previous lectures incorporated:

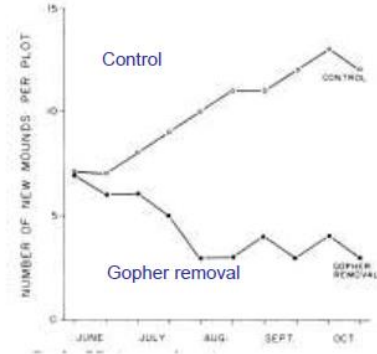
- Abiotic conditions and stress → desiccation of seeds
- Age-structure and life history → delayed iteroparity brings vulnerability
- Species interactions → predation by gophers
- Evolutionary ecology of dispersal → why no elaisomes? → elaisomes encourage dispersal by ants → most plants do better when dispersed away from parents, but for glacier lilies, staying close = ↓ predation
- Patchy, heterogeneous landscapes exert heterogeneous pressures (what happens in one habitat may not happen in another)

Aspen trees

- Now “zoom out” to landscape level → aspen-meadow matrix
 - Why is it patchy?
 - Why isn't it all aspen or all meadow?



- Recall: aspen trees are clones, roots grow underground and put out new shoot few metres away
- **Cantor and Whitman Aspen-Gopher Experiment**
 - o Gopher removal experiment
 - o ↓ gophers = ↑ aspens
 - o Aspen grow better in deep-soil areas but only if protected from gophers (like glacier lilies)
 - o Aspen clones centred on rock outcrops → outward expansion limited by gophers cutting roots
 - o ∴ **Rock-refuge hypothesis** again
- Gophers prevent aspen from invading meadow and pushing out other species
- ∴ Pocket gophers are **keystone species** or **ecosystem engineers** → control aspen-meadow matrix (prevent meadow from becoming forest)



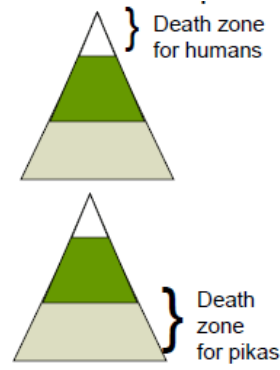
Gopher effects

- Gophers have **direct negative** effect on lilies → eat them
- Gophers have **indirect positive** effect on lilies and hundreds of other species in meadow that are sun-requiring → act as **disturbance to prevent succession** from turning meadow into forest (prevent aspen invasion)
- Indirect effects outweighs direct effects

Climate change

- Increased atmospheric concentrations of carbon dioxide, methane and others are **trapping more solar heat** (anthropogenic causes mostly)
- On avg, atmosphere is warming and can hold more water
- Circulation patterns changing (i.e. Hadly cell gets stronger/larger → desert belts shifting poleward beyond 30 degrees)
- Local climate changes affect organisms
- Geographical ranges are shifting to match ranges of tolerance → migration to colder area
- For some species, this migration is considerably easy
- However, animals most affected are those w/ nowhere to migrate to (already at high latitude/altitude)
- Ex. Arctic ice melting, polar bear habitat shrinking → polar bears already at highest latitudes, cannot move anywhere colder
- Polar-grizzly bear hybrid found, so although polar bear may go extinct its genes may remain in hybrid animals

- Ex. Pikas adapted to cold mountain tops, cannot travel down mountain and across deserts (too hot → die) to find another mountain
- Study resampled 25 mountain ranges in which pikas had been found earlier, pikas disappeared in 7/25



Lecture 12: Introduction to Evolutionary Biology

Introduction to study of evolution

- Focus on “population” level of biological organization → primary unit of evolution
- Individuals cannot evolve (same genes throughout life), only populations evolve

Scope of question:

- **Small** – answering small tractable questions contribute towards solving a big question
- **Large** – unlikely to be answered by one experiment, requires multiple lines of evidence (Ex. Why did sex evolve? Why is most biodiversity in tropics?)

Type of question:

- **How (proximate)** – involve determining **physiological** or **genetic mechanisms** responsible for aspects of trait
- **Why (ultimate)** – involve determining **ecological function** or **adaptive significance** of trait

Approaches used in evolutionary biology

1. **Observational** – describe and quantify
2. **Theoretical** – develop models (verbal, graphical, mathematical)
3. **Comparative** – obtain same data from many species
4. **Experimental** – manipulate system to address specific hypothesis, requires an experimental design and statistical analysis

Assumptions in evolutionary biology

1. Organisms on earth have **changed** through time (99% of species ever to live on earth are extinct)
 2. The changes are **gradual**, not instantaneous
 3. Lineages split or branch by **speciation** resulting in generation of biodiversity
 4. All species have **common ancestors**
 5. Most evolutionary change results from **natural selection** – the only process responsible for the evolution of biodiversity and adaptation
- *Assumptions have been verified by scientific study
*Biodiversity and adaptation are products of evolution

Biodiversity: variety of life on earth; the number and kinds of living organisms in a given area

Adaptation: two meanings (state or process)

- Any trait that contributes to fitness by making organism better able to survive or reproduce in given environment
- The evolutionary process that leads to origin and maintenance of such traits

Theory of evolution

- **Central unifying concept** of biology
- Affects many other areas of knowledge
- One of most influential concepts of Western thought
- “Nothing in biology makes sense except in the light of evolution” – **Dobzhansky** (fruit fly geneticist and founder of modern evolutionary synthesis)

Sub-fields of evolutionary biology

1. Microevolution – evolutionary mechanisms

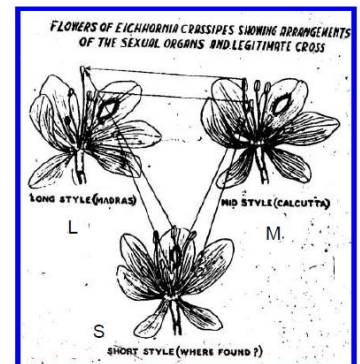
- Determining ecological and genetic **mechanisms responsible for evolutionary change**
- Involve population-level studies of natural selection, adaptation and speciation using diverse organisms
- Testing of theoretical models by experiments in the laboratory or field
- Largely **process orientated** and **experimental**

2. Macroevolution – evolutionary history

- Determining evolutionary **relationships** of organisms in terms of common ancestry – phylogenetics
- Affinities of organisms provide a basis for **classification** – taxonomy and systematics
- Comparative data from many sources (ex. biogeography, paleontology, morphology, development and genomics)
- Largely **pattern-based** and **non-experimental**

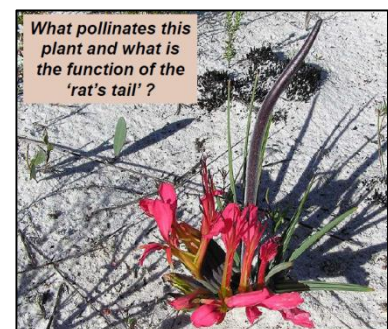
Biodiversity and adaptation study: example water hyacinth

- **Water hyacinth** = world's most serious aquatic weed, blocks rivers and drainage canals
- Sexual (left) and clonal (right) reproduction
- Blocks rivers largely by **clonal propagation**
- Darwin determined 3 sexual types for plant → short/medium/long styled
- But only M and L morphs were evident, **missing S morph**
- Prof found S morph in amazon during undergrad studies
- Believed plant was originally from amazon → found S/M/L morphs here
- S morph restricted to Lowland S. America (native range) → example of strong founder event
- **Founder event**: introduction of small number of individuals that possess small sample of genetic diversity of source population
- ∴ Human introduction of plant to alien range had only M/L genes, that's why S morph thought to be "missing"
- Recent survey of genetic diversity of plant found greatest biodiversity (i.e. S/M/L morphs) in amazon, almost no biodiversity in China/elsewhere



Biodiversity and adaptation study: example rat's tail perch

- Rat tail plant has bright flowers → bright flowers usually to attract birds
- **Bird pollination** evolved independently in many lineages of angiosperms
- In New World, hovering birds do most pollination (ex. hummingbirds)
- In Old world, perching birds do most pollination
- Perching birds in Africa → infer rat's tail is perch
- **Observational approach**: observed malachite sunbirds would perch by grabbing rat's tail and hanging upside down to feed on nectar
- ∴ Rat's tail serves as **bird perch** to facilitate nectar feeding
- **Experimental approach**: removal of perch = dramatic reduction in bird pollination → lowers fertility and increases **self-fertilization**
- ∴ Perch is adaptation promoting plant **reproductive success**



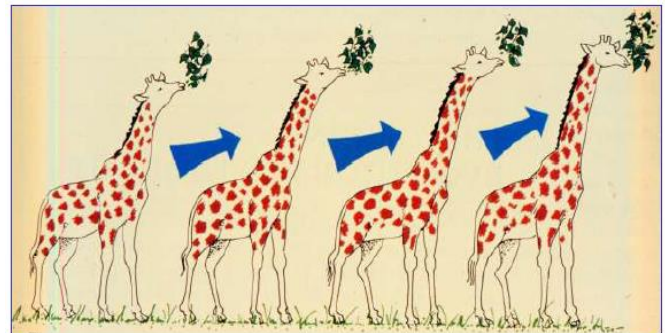
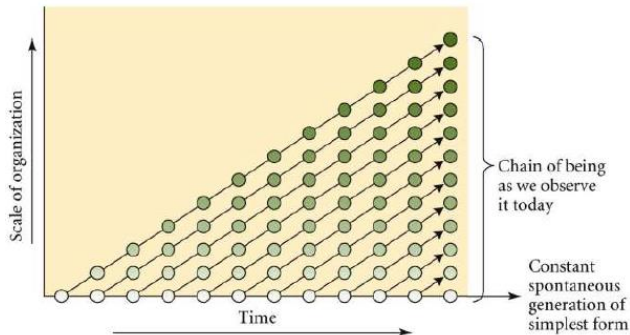
Lecture 13: Darwin's Big Idea and How It Changed Biology

Theory of evolution

- Living things **change gradually** from one form into another over time
- Challenges view of special creation (direct creation of all things in effectively their present form)
- Involves two controversial ideas:
 1. Concept of changing universe (replaced view of static world)
 2. Phenomenon with no purpose (replaced view that everything has purpose)

Lamarck

- First to use term evolution
- First to provide casual mechanism → **inheritance of acquired characters**
- **Lamarck evolution**: idea that individuals acquire characteristics throughout lifetime and pass on to offspring
- But proposed **wrong mechanism** → linear rather than branching view of evolution
- Said simplest forms evolve directly into complex forms (all individuals on same path that ends in same complexity) → **lineal descent** (no evolutionary tree)
- Ex. If giraffe spends whole life stretching neck to reach food, neck will get longer and offspring will have long neck
- Ex. If alchemist spends whole life hitting metal and making metal, will get big muscles and son will have big muscles



Weismann: proving Lamarck wrong

Weismann **germplasm theory**:

1. Inheritance only by germ cells (gametes), somatic cells (soma) do not function as agents of heredity
2. Thus genetic information cannot pass from soma to gametes and onto next generation
3. Modern interpretation stated in molecular terms: genetic information flows in one direction → DNA to protein, never in reverse

Wallace and Darwin: co-discovery

- Co-discovery of correct mechanism of evolution: **natural selection**
- Both came up w/ theory independently
- Wallace inspired by Darwin's "The Voyage of the Beagle" to travel

- Wallace collected rare specimens to sell, not for scientific study like Darwin
- In Asia, Wallace noticed variation in species
- When returned, wrote manuscript about it and sent to Darwin (his hero)
- At same time, Darwin working on same theory (Darwin returned from Beagle)
- But Darwin working very slowly and meticulously → wanted to “get it right” b/c knew it would be unsettling, especially for church

Timeline for publication of Origin of Species

- Darwin back from Beagle for 20 years now → spent time accumulating evidence for theory
- **1844**: wrote but did not publish essay on natural selection → proves Darwin developed idea of natural selection independently from Wallace, did not steal Wallace’s idea
- **1856**: began work on natural selection book
- **June 1858**: received natural selection manuscript from Wallace (“On the tendency of varieties to depart indefinitely from the original type”)
- Obviously big deal, but Darwin ok with publishing idea as co-authors
- **July 1858**: Darwin-Wallace paper presented at Linnean Society in London, neither Darwin or Wallace were there b/c Wallace in Asia and Darwin didn’t want to present w/o Wallace
- Paper did not receive too much recognition, motivated Darwin to finish his book
- **1859**: publication of “The origin of species by means of natural selection or the preservation of favoured races in the struggle for life”

The Origin of Species

Two key components:

1. **All organisms have descended with modification from common ancestors**
2. **The major agent of modification is natural selection operating on variation among individuals**

Darwin’s influences leading to development of ideas of evolution

1. *Family*

- Grandfather got Darwin interested in plants/animals
- Father had collection of orchids
- At young age Darwin asked to make notes about when orchids flowered

2. *Exploration*

- Parents wanted Darwin to be doctor, couldn’t handle blood
- Next did divinity studies at Cambridge → met botanist **Henslow**
- Henslow took Darwin on outdoor trips, saw Darwin was interested in natural history
- Henslow asked Darwin to voyage around world for 5 years and be natural historian
- Purpose of voyage was to map continents of world (particularly S. America) and Darwin’s job was to collect stuff
- **Voyage on Beagle** around world (1831-1836) as ship’s **naturalist**
- Made numerous observations and collections of plants, animals and fossils
- Returned to England and spent rest of life in seclusion at Down House → developing ideas, conducting experiments and writing books (25 total)

3. *Gradualism*

- Darwin read **Lyell**'s book "Principles of Geology" (1830)
- Lyell said present day landscape molded by geological processes over long period of time
- Can explain history of earth by geological processes → "**gradualism**"
- Notion of dynamic rather than static world emerged in Darwin's thinking (dynamic but still slow, i.e. life evolves very slowly)

4. *Species variation*

- Observed **variation patterns in Galapagos mockingbirds**
- Could not distinguish "boundaries" b/w collected species
- Could not sort into what was supposed to be 4 similar species → species were endemic to islands and descended from S. American mainland ancestor
- Made Darwin **doubt fixity of species** → species are not fixed entities w/ specific set of characteristics
- Challenged notion of "typological" species (i.e. species can be represented by perfect type)
- Species can merge into one another, variation within species (subspecies, races)

5. *Selection*

- Darwin read **Malthus**' "Essay on the Principle of Population" (1798) in 1838
- Malthus said human populations would reach carrying capacity, after which struggle for existence (limited resources) → individuals w/ characteristics that make them better at getting resources more likely to survive
- Very similar to natural selection
- Darwin says: "It at once struck me that under these circumstances **favourable variations would tend to be preserved** and unfavourable ones would be destroyed"

Darwinian thinking

- Recognition that variation among individuals is not imperfect, but material from which natural selection fashions better adapted forms of life
- Involves moving away from typology and notion of ideal species to population thinking

Requirements for evolution

1. **Variation** – variation among individuals in a population
2. **Heredity** – progeny resemble their parents more than unrelated individuals
3. **Selection** – some forms are better at surviving and breeding than others in a given environment

Creation "science" is not science

- Creationist doctrine = literal reading of *Book of Genesis* (creation of all living organisms by divine order in 6 days, all organisms individually created and designed by purposeful creator)
- Anyone who believes *Genesis* as literal description of history holds world view that is incompatible w/ evolution and science itself
- **It is not science b/c:**
 - Not supported by any empirical observations
 - Does not infer its principles from observation (as does all science)
 - Its assumptions lead to no testable or falsifiable hypotheses

Lecture 14: What Darwin Saw – A Geographical Perspective on Biodiversity and Adaptation

Temperate ecosystems

- Low biodiversity
- Mainly abiotic factors

Tropical ecosystems

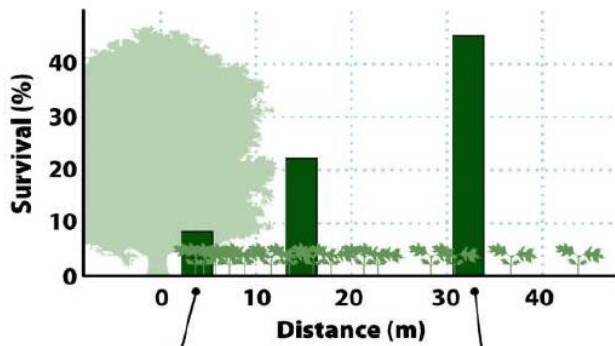
- Very high biodiversity
- Mainly **biotic factors**, esp. coevolved **plant-animal mutualisms**
- Year-round warmth and rainfall = rapid species growth of insect and microbial populations
- Intense disease and **pest pressures** on plants
- First stop for Beagle is Brazil

Pollination in tropical ecosystems

- High biodiversity in rainforest (up to 300 tree species) → **individuals of same species widely separated**
- Trees can flower individually, km away from nearest tree of same species
- Darwin wondered how trees could pollinate/reproduce
- In temperate ecosystems, same species of trees close together → wind main pollinator
- But in evergreen rainforests w/ dense canopies and long distance b/w trees, **wind ineffective**
- Animals capable of flying long distance can pollinate trees (ex. birds, bees, butterflies, bats)
- **Janzen** used mark-recapture techniques to show bees and other flying animals travel long distances in foraging trip → “**trapline foraging**”

Pest pressure in tropical ecosystems

- Pest pressure so strong in tropical ecosystems that there is negative relationship b/w seedlings and distance they land from tree
- Janzen’s pest pressure hypothesis: **tropical tree seedlings less likely to survive and establish close to maternal parent**
- Confirmed through field experiments
- ∴ Methods of long distance pollination needed → dispersal very important in tropical ecosystems
- Intense herbivory in tropical ecosystems results in considerable damage and consumption of plant biomass (ex. giant amazon water lily)



Seedlings are most dense close to the parent tree...

...but survival of seedlings is highest at a distance from the parent.

Mutualism: example ant and pea plant

- Pea plant has thorns w/ **nesting sites**



for ants

- Also **extrafloral nectaries** (sugar) and **beltian bodies** (protein) for ants
- Plant providing home and nutrition for ant → must be mutualistic relationship
- Janzen did ant removal experiment using tangle foot chemical that deters ants but not other bugs → in a couple of weeks, pea plant completely defoliated by beetles
- ∴ **Ants protect plants against herbivorous insects**

Mutualism: example ant and devil's garden plant

- Devil's garden has bare area surrounding it
- Plant provides **nesting site** for ants
- Ants spray **formic acid** (natural herbicide) on weeds to prevent them from growing and outcompeting devil's garden
- ∴ **Ants protect plant being outcompeted**



Epiphytes

- Common in tropics
- Capture water/insects through aerial roots
- Epiphytic life form evolved independently in many unrelated families (ex. epiphytic bromeliads, epiphytic lichens, etc) = "**convergent evolution**"
- Some questions in studying epiphytes
 - o Are particular trees favoured?
 - o How are they dispersed? (Answer: fleshy fruits eaten by birds)
 - o What pollinates them? (Answer: hummingbirds)



In the wild



Berlin Botanical Garden

Biodiversity in tropics so high → countless opportunities to investigate functions and adaptive significances:



Preying mantid: camouflage tactic?
Katydid: camouflage tactic?
Red bracts: attract pollinators?
Two-colour flower: attract pollinators?
Juvenile red leaves: insects do not see red as well so deters from eating young leaves
 *All can be



experimented

Patagonia

- After Brazil, Beagle heads south to Patagonia
- Completely different landscape →

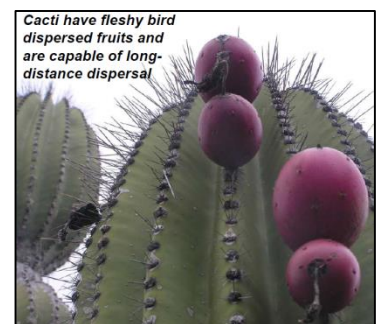
cold, windy, geologically young

- Severe climate = ecosystem dominated by **abiotic factors**
- Noticed abrupt tree line
- Saw animals similar, yet different:
 - o Ex. black-necked swan
 - o Ex. Dark-coloured bumblebees
- Saw animals completely different:
 - o Ex. Guanaco (related to camel)
 - o Ex. Darwin's rhea (flightless bird)
- Made Darwin think about species related around world



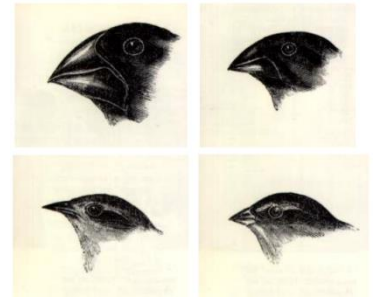
Galapagos Islands

- After Patagonia, Beagle heads to Galapagos Islands
- Spent only 5 weeks on islands but most important time → observations formed foundation for theory of evolution
- 15 main islands of volcanic origin; oldest 5-10 million years old (geologically very young)
- Flora and fauna **colonized by species capable of long-distance dispersal** from South American mainland (flying, drifting on logs → no large mammals)
- Darwin saw **races** and **sub-species** on different islands → provide evidence of early stages of **speciation**
- Prickly pear cacti first colonizers → got there by their fruit (eaten by birds and excreted on islands)

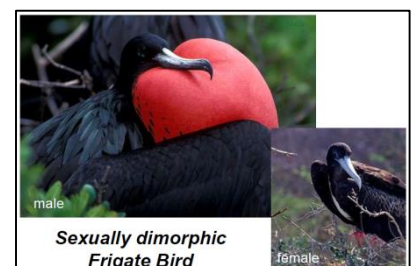


Darwin's finches

- Not as influential as everyone thinks
- Darwin actually made mistake → collected finches but did not record from which islands
- However he did sketch different beaks → **speciation**
- Prompted **Peter & Rosemary Grant** to do 35 yr study on finches
- Found 14 different species of Galapagos finches → represents adaptive radiation



- **Adaptive radiation**: evolution of ecological and phenotypic diversity within a rapidly multiplying lineage as a result of speciation; from a single common ancestor the process results in array of species that differ in traits allowing exploitation of a range of habitats/resources
- Features identifying adaptive radiation:
 1. **Recent common ancestry from single species**
 2. **Phenotype-environment correlation**
 3. **Trait utility**
 4. **Rapid speciation**
- Darwin also observed **differentiation** in giant tortoises: tortoises on diff islands have diff shell patterns (10 subspecies of a single species)
- Observed differences in iguanas: marine iguanas eat seaweed (white patch is special gland that expels salt), land iguana eat prickly pear
- Typically **flightless birds** on islands
- Huge **sexual dimorphism** (males/females look very different)



Australia

- After Galapagos Islands, Beagle heads to Australia
- Distinct flora/fauna with high levels of **endemism** (species restricted to particular geographical region or habitat)
- Biological uniqueness due to long history of **geographical isolation** from other land masses
- Although a continent Australia also an island → shows many island characteristics (ex. endemism, radiation, unique adaptations)
- Species in Australia look similar to those in Amazon, but different (ex. epiphytes)

- Very different forests than amazons → dominated by one genus of trees (eucalyptus/gum tree) = **low biodiversity, dry forests**
- Unique adaptation example: koala has specialized diet of eucalyptus leaves, can detoxify chemicals that are toxic to other animals
- Rodent pollinated plants (picture)



Lecture 15: Neo-Darwinism and The Evolutionary Significance of Genetic Variation

Recall: Requirements for Darwin's Theory of Evolution by Natural Selection

1. **Variation** (genetics)
2. **Heredity** (genetics)
3. **Selection** (ecology)

*Darwin had no understanding of genetics and mechanism of inheritance

Genetics terminology

- **Gene** (various definitions):
 - o Functional unit of inheritance
 - o Unit of hereditary information located on chromosomes consisting of DNA
 - o DNA sequence composed of codons (sequence of 3 nucleotides) essential for specific biological function
- **Genotype**: genetic constitution of an organism, used in relation to particular gene or gene combinations (ex. Aa, AaBB)
- **Phenotype**: the organism as observed, used when discussing a trait or feature of an organism that varies
- **Genome**: the entire organism's DNA including both genes and non-coding regions

Sources of genetic variation

1. **Mutation** (focus of lecture)
 2. **Recombination**
 3. **Gene flow**
 4. **Hybridization**
- Recombination is enormous source of genetic variation
 - Most genetic variation results from sexual reproduction → recombination and independent assortment during meiosis
 - Ex. humans w/ $n=23$ chromosomes, 2^{23} = over 8 million possible gamete combinations
 - Mutations account for rather small amount of genetic variability (b/c mutation rates are low)

Mutations

- Stable change in DNA sequence resulting in change of genotype
- Unstoppable phenomenon (despite cellular mechanisms to correct errors during DNA replication)
- Occurs at very low but **variable rate** in all organisms
- Rates depend on type of mutation, also varies among gene
- Environmental insults can affect mutation rate (ex. mutagens, high temp)
- Not directed by organism or environment → occur randomly
- To be evolutionary significant, must occur in **germ cells** (somatic mutations not inherited)
- Can be **neutral**, **beneficial**, **deleterious** or **lethal** → often depends on environment
 - o Beneficial → lead to evolution (speciation)
 - o Lethal → usually eliminated by natural selection

Kimura: neutral mutations

- Before Kimura, mutations were thought of as either good or bad
- Kimura recognized that many mutations in genome are neutral
- Also said effects of mutations are different in diff environments
- Ex. flies w/ certain mutation ok at 20 degrees, but at 30 degrees mutation turns lethal and kills them all

McClintock: jumping genes

- Studied mobile genes in maize
- Involve **transposable** genetic elements that can move around genome
- Chunk of DNA removes itself from where it is and inserts itself somewhere else in genome
- Arise by mutations

Types of mutations

1. Point mutations

ATGCAGT → ATCCAGT

2. Insertions/deletions (including “jumping genes”)

ATGCAGT → ATGGCAGT

3. Changes in repeat number

ATGATGATG → ATGATGATGATG

4. Chromosomal rearrangements (very serious)

ATGCAGT → TGACGTA

Mutation example: *Drosophila* fruit fly

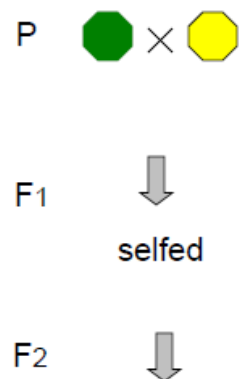
- Simple recessive mutation (red vs. white eye)
- **Homeotic mutation** (leg where antenna should be)

Mutations in humans

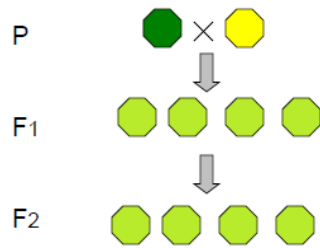
- Most of us carries 3-5 **recessive lethal** alleles
- Lethal alleles cause death when homozygous → why inbreeding w/ family causes mutations
- Mating among relatives = higher incidence of offspring mortality

Mendel: mechanism of inheritance

- Experiments using controlled crosses w/ peas
- Laws of inheritance or “Mendel’s Laws”
- Mendel’s experiment:
 - o P (parents): cross b/w two pure-breeding lines
 - o Parental plants differ in some observable phenotypic trait (ex. flower colour, plant height, seed shape)
 - o Look at next generations (F₁, F₂, etc.)



- **Blending inheritance** predicts offspring of cross should show intermediate phenotype:



- But results inheritance
- Instead to

did *not* conform to predictions of blending

parental phenotypes retained from generation generation:



In above example,

- Yellow **dominant** to green which is **recessive**
- Predictable **3:1 phenotypic ratio**
- Predictable **1:2:1 genotypic ratio** in F₂

Conclusions from Mendel's experiment

- Inheritance determined by discrete particles (**genes**) → “**particulate inheritance**”
- Most organisms carry 2 copies of each gene (**alleles**) = **diploid**
- Organisms produce **gametes** (sperms/eggs) each containing one allele
- Gametes = **haploid**, how we inherit genes
- Offspring inherit one allele from each parent at **random**
- ∴ Everyone has 2 copies of each gene → can be heterozygous, homozygous dominant or homozygous recessive
- Meiosis and recombination important b/c prevents “build-up” of genome (alternate b/w haploid → diploid so that chromosome number stable)

Discrete trait

- Aka “Mendelian trait” → classic Mendelian genetics
- Simple inheritance by 1/2 major genes
- All individuals can be put into discrete categories (i.e. grey or white, striped or not striped)
- **Genetic polymorphism** = when two or more discrete forms of species in same locality in such proportions that the rarest form > 5% occurrence
- Genetic polymorphism involves discrete phenotypes (“morphs”) governed by segregation of small number of alleles at 1-2 major genes
- Ex. polymorphism for flower colour of wild *Gladiolus*



Continuous trait

- **Continuous trait**: complex inheritance by many genes (polygenes) of small effect → **quantitative inheritance**
- Quantitative inheritance includes many genes and usually interacts w/ environment
- Ex. height → variation in human height caused by 65% genes, 35% environment (why children are not always intermediate height b/w parents)

Discrete traits

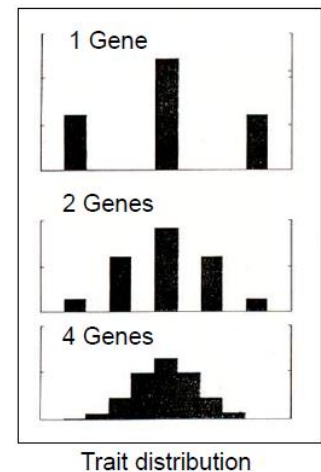


Continuous traits



Gene number and phenotypic distribution

- Generally, \uparrow **number genes** = \uparrow **distribution**
- Few genes → discontinuous (discrete) variation
- Many genes → continuous variation
- *Note: 1 gene graph illustrates **co-dominant gene** (heterozygote has intermediate phenotype b/w homozygous phenotypes) → not just dominant and recessive



Genetic analysis of variation (areas of research)

1. *Discontinuous variation (Mendelian genetics)* → major genes, dominance and recessiveness, genetic polymorphism
2. *Continuous variation (quantitative genetics)* → polygenes, selection response, artificial selection experiments

Fisher: Fundamental Theorem of Natural Selection

- Rate of evolution (how fast population adapts and evolves) is mathematically predictable based on amount of variation in population
- Amount of genetic variation in population will determine how quickly a population can adapt
- Leads to next lecture → how to measure genetic variability?

Lecture 16: The Maintenance and Measurement of Genetic Variability

Foundations of population genetics

- 1930-1950: **Fisher**, **Haldane** and **Wright** provided foundations for “**Neo-Darwinism**” or “**new synthesis**” (synthesis of Darwin’s theory with genetics)
- Showed Darwinian natural selection and continuous variation consistent with Mendel’s laws
- Also demonstrated significance of genetic variation

Parameters of genetic variation

1. **Polymorphism (P)** – proportion of gene loci that are polymorphic
2. **Heterozygosity (H)** – average frequency of heterozygous individuals per gene locus

Processes affecting genetic variation

1. **Mutation** (↑): random errors during replication → ultimate source of genetic variation
2. **Recombination** (↑): introduces new combinations of mutations into population
3. **Genetic drift** (↓) random sampling effects every generation, important in small populations
4. **Natural selection**
 - a) *Adaptation* (↑): mutations that increase fitness become fixed
 - b) *Purifying* (↓): mutations that reduce fitness removed by selection
 - c) *Balancing*: maintains diversity (i.e. when mutation arises but does not replace pre-existing variance at locus)

Classes of explanations to how genetic variability is maintained

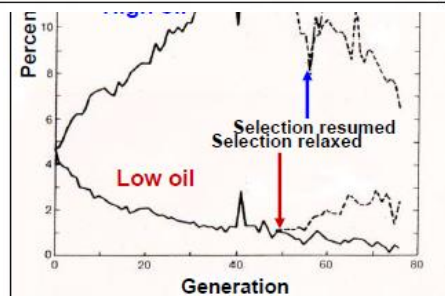
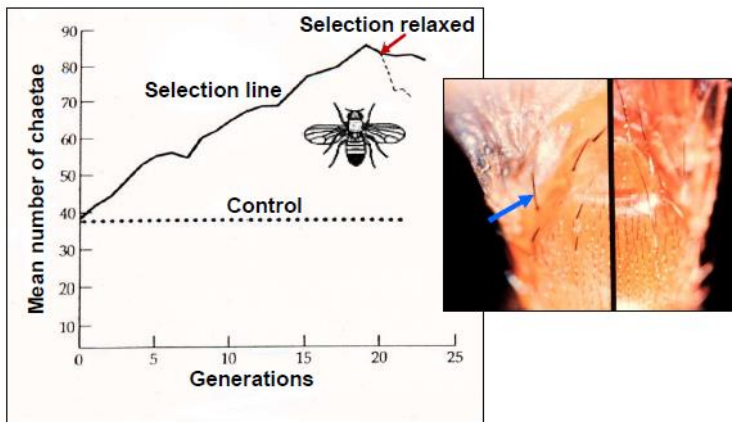
- **Mutation-selection balance**
 - Balance b/w mutations bringing in alleles and selection taking them out
 - Less fit genotypes maintained by repeated mutation
- **Selective forces**
 - **Heterozygote advantage** → if heterozygote fitter than either homozygotes, variability maintained
 - **Frequency-dependent selection** → fitness depends not only on organism, but frequency of other organisms (ex. sex ratio: many males but not enough females, ∴ competition for males to mate)
 - **Fitness varies in space and time** → certain genotypes do better in different environments/times (environment is heterogeneous)
- **Variation selectively neutral**
 - Some mutations neutral → do not affect fitness
 - Genetic variability maintained simply b/c neutral mutations not taken out by selection

Early evidence for existence of genetic variation

- Human imposed selection
- Selection experiments on **quantitative traits** (not Mendelian traits) in different groups of organisms
- Involves controlled breeding and selection of individuals for many generations
- Called **artificial selection**

Artificial selection experiment example: *Drosophila* bristle numbers

- Selection for hairs (**chaetae**) on fruit flies
- Selection line → top 5% of flies w/ most chaetae selected to breed together every generation
- Control line → random mating
- **Selection response** → increasing selection line means there was genetic variation for chaetae number in starting population
- Important experiment b/c exposed fact that there is genetic variability

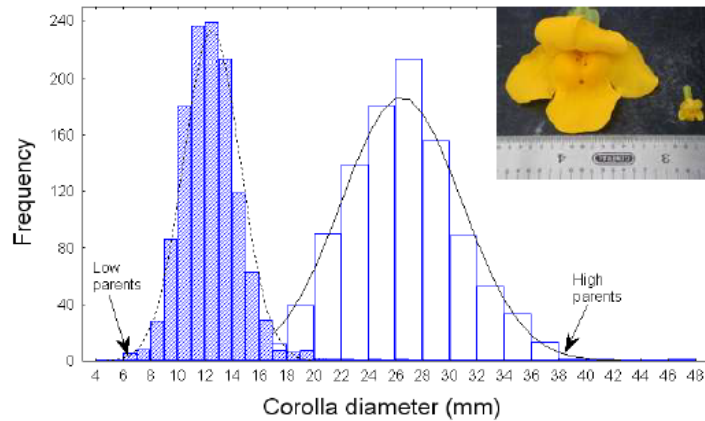


Artificial selection experiment example: oil % in maize seeds

- Longest artificial selection experiment ever
- Selected for high oil and low oil, relaxed/resumed selection at various times (same concept as above)
- Selection response shows there is genetic variability

Artificial selection experiment example: large and small monkey flowers

- Selected for large flowers and small flowers (same concept as above)
- Selection response shows there is genetic variability
- Abundant quantitative genetic variation for flower size maintained in natural populations
- Found enough variation in one population to produce variation seen in entire species

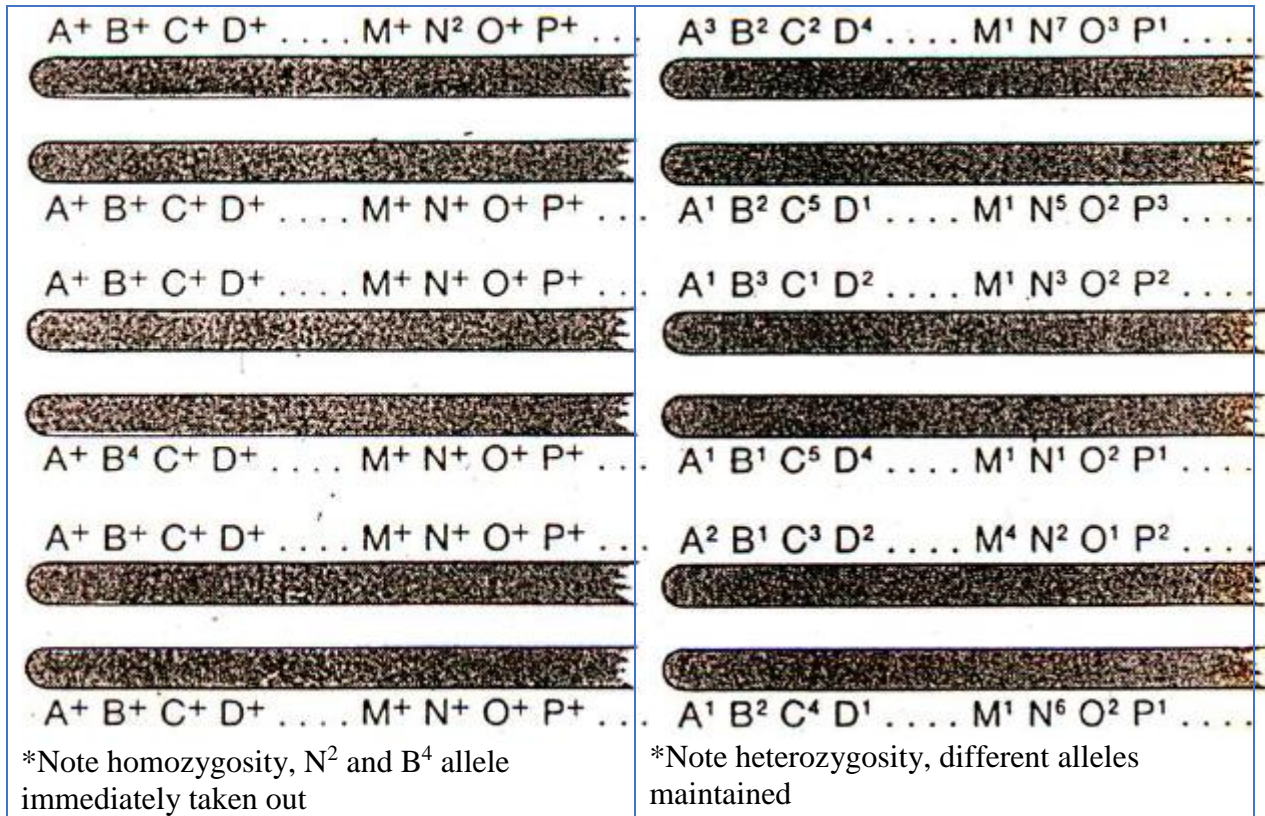


Conclusions of artificial selection experiments

- Selection responses demonstrate abundant genetic variation exists for polygenic (quantitative) traits
- But no information on key population genetic parameters (P, H)
- Also can't generalize b/c experiments were group specific
- Lead to problem: how do we quantify variation for any species?

Models of population genetic structure

Classical school	Balance school
<ul style="list-style-type: none"> ▪ Morgan, Muller ▪ Lab mutants ▪ High homozygosity ▪ Low polymorphism ▪ Wild type is best genotype ▪ Purifying selection reduces diversity 	<ul style="list-style-type: none"> ▪ Ford, Dobzhansky ▪ Natural populations ▪ Low homozygosity ▪ High polymorphism ▪ No best or ideal genotype ▪ Balancing selection favours diversity



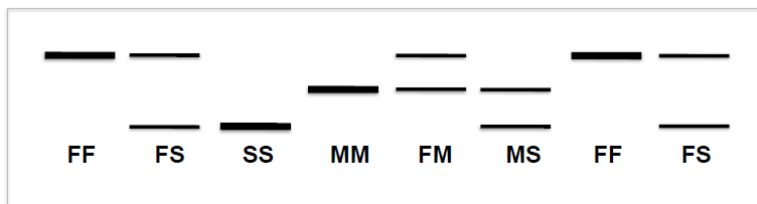
Lewontin: gel electrophoresis

- Allows quantifying H and P
- Gel electrophoresis of allozymes (different forms of same protein)
- Measure diversity at genes controlling **enzymes** and **proteins**
- Can determine proportion of variable (polymorphic) genes → dispute b/w classical and balance schools

Monomorphic gene



Polymorphic gene



- Results conformed to balance school

All homozygous fast
No genetic variability → every individual has same 2 alleles

Homozygous fast, medium, slow
Heterozygous fast/medium/slow combinations

∴ genetic variability!

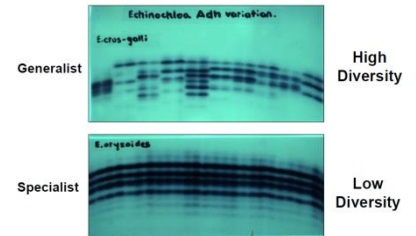
Advantages of enzyme/protein polymorphisms

- Can be used in nearly **any organism** (all organisms have genes, all produce enzymes/proteins)

- Variation examined close to DNA level, many loci can be examined
- Can literally count genotypes → count heterozygotes → witness **co-dominance** (not just dominance and recessiveness)
- Provides **genetic marker** loci for other studies
- Note: variation measured largely neutral (i.e. not under selection)
- Studies of quantitative inheritance still necessary to determine how much variation occurs for ecologically-relevant traits (i.e. under selection) → ex. size, fecundity, other life-history traits

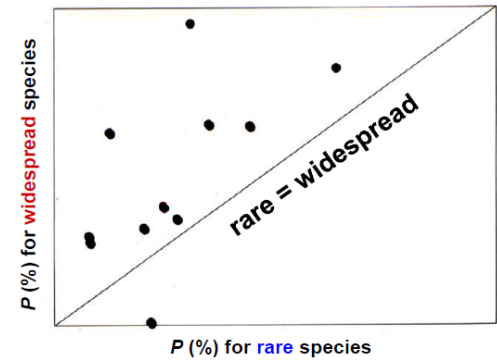
Electrophoresis example: barnyard grasses

- **Generalist**: high diversity
- **Specialist**: low diversity



Polymorphisms in rare vs. widespread plant species

- Polymorphism (P) compared in rare vs. widespread species in 11 genera
- In all genera but one, higher P in widespread species
- Indicates **rare species** have **low genetic diversity**

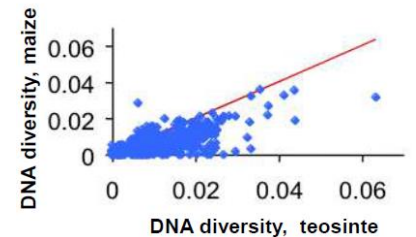


DNA sequencing

- Allows differences b/w individuals in single nucleotides to be identified
- SNP's = single nucleotide polymorphisms, can be measured for thousands of genes
- Can compare organisms: DNA polymorphism in fruit fly (1/20 bp) vs. DNA polymorphism in humans (1/1000 bp)

DNA sequencing example: maize vs. teosinte

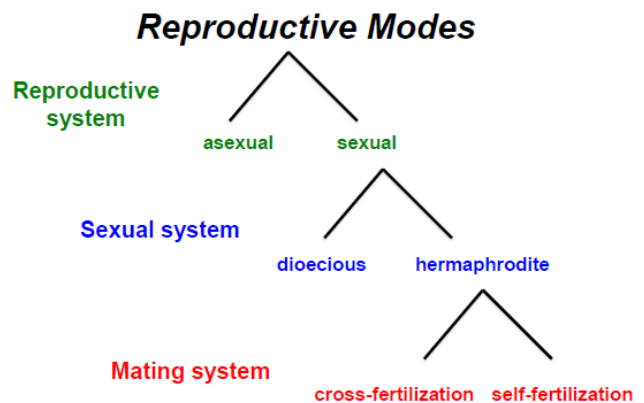
- **Wright** found that domestication of maize from its progenitor teosinte caused 57% reduction in variation at SNP's
- Estimate that 1200 genes have been affected by artificial selection



Lecture 17: Organismal Reproductive Diversity

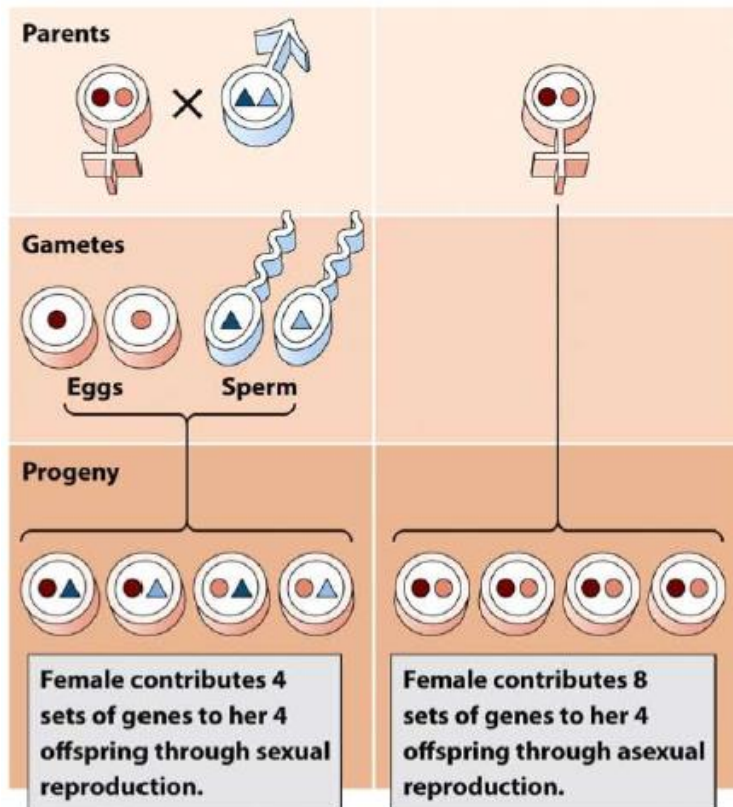
Reproductive modes

- **Dioecious**: individual male and female organisms (majority of species)
- **Hermaphrodite**: individuals that perform both as males and females
- Ex. water fleas *Daphnia* → sexual in warmer, turbulent water; asexual in cooler, calm water
- Ex. water hyacinth → both sexual and clonal reproduction



Costs of sex

- Time and energy to find and attract mates
- Increased energetic costs
- Risk of predation and infection
- Cost of producing males
- Break up of adaptive genes combinations
- **50% less genetic transmission** (most important from genetic viewpoint → if individual has high fitness, why not pass on 100% of genes to offspring, rather than risk combining genes with less fit individual?)



Sexual female contributes only 50% of her genes to next generation compared with asexual female

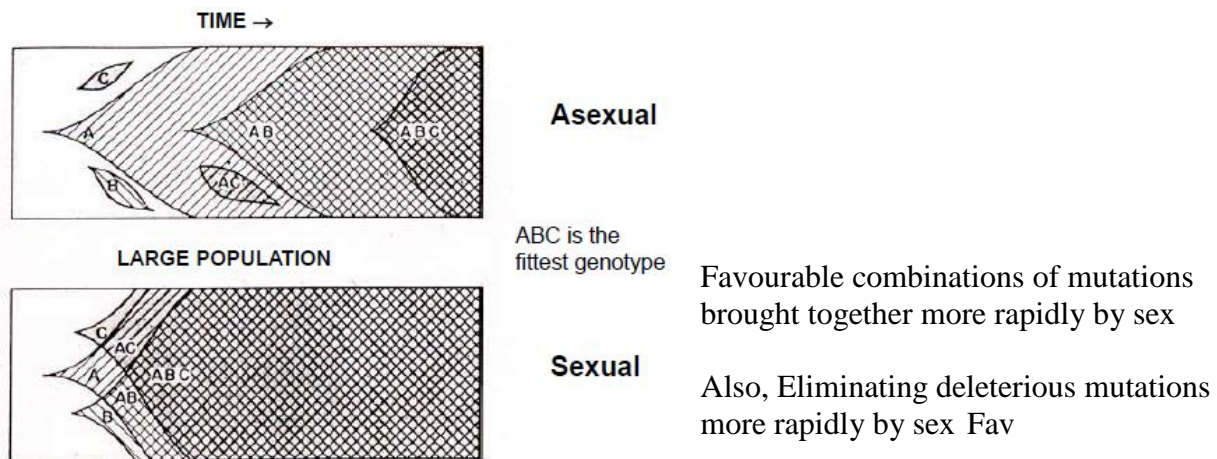
Called “**transmission bias**” favouring asexuals

Since so many costs of sex, why did it evolve and why was it maintained? Researchers:

- Aneil Agrawal
- Graham Bell
- Sarah Otto

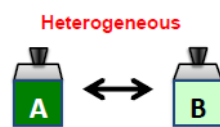
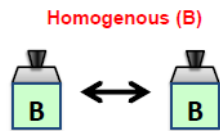
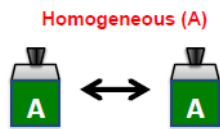
Hypothetical advantages of sex

- Bringing together favourable mutations (long term benefit)
- Benefits of genetic variation in variable environments (short term benefit)
 - Called “lottery model” → is it better to buy 1000 different lottery tickets or 1000 copies of the same ticket?
- **Tangled bank hypothesis**: spatially heterogeneous environments
- **Red queen hypothesis**: temporally heterogeneous environments (i.e. some organisms evolve faster than others → co-evolutionary race)

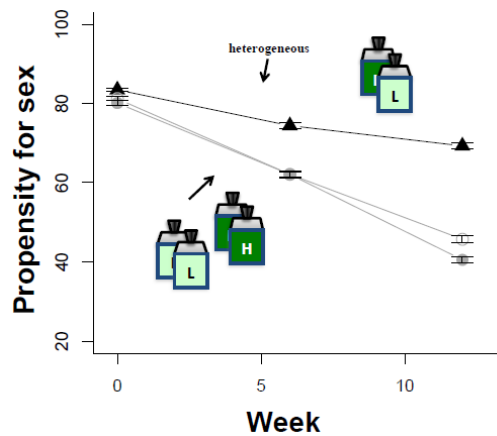


Spatial heterogeneity example: *planktonic freshwater animal*

- Theory predicts spatial heterogeneity in selection can facilitate evolution of sex
- **Agrawal** and **Becks** studied planktonic freshwater animal → facultatively sexual with genetic variation for propensity to reproduce sexually or asexually
- Each population consisted of 2 subpopulations, with migration performed manually b/w them
- Over 12 weeks (~70 generations), sex declined rapidly in homogenous environments but persisted at much higher level with spatial heterogeneity
- ∴ **Higher rates of sex maintained in populations evolving in heterogeneous habitats**



Evolutionary asexuality
- Asexuality



history of

distributed

(**parthenogenesis**) sporadically across animal kingdom

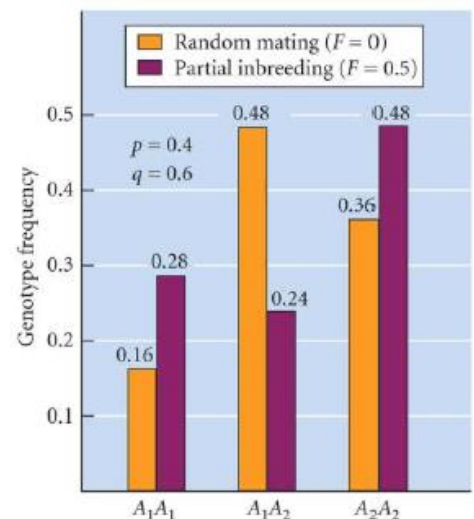
- More common in invertebrates, rare in vertebrates
- Asexuality (**clonal propagation**) much more common in plants, although few species (if any) are exclusively asexual
- Ex. *Bdelloid rotifers* exclusively asexual for millions of years (only known species) → implies disadvantage of asexual reproduction b/c all other species have sex
- Asexual species usually at tips of phylogenies → **long-term evolutionary potential low** due to **lack of genetic variation**

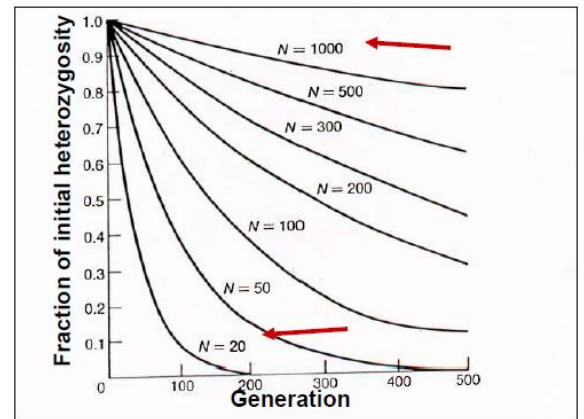
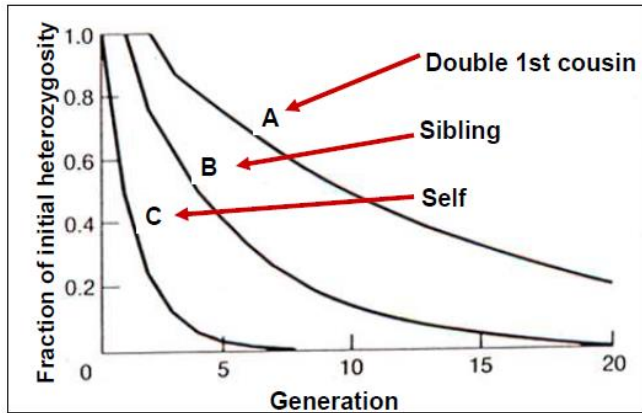
Mating patterns

- **Outbreeding**: mates less closely related than random
- **Inbreeding**: mates more closely related than random
- Usually continuum b/w outbreeding and inbreeding

Genetic consequences of inbreeding

- Genotypic frequencies changed (right graph)
- Allele frequencies not changed, just redistributed (heterozygous → homozygous)
- Results in **↑ homozygosity**, **↓ heterozygosity**
- Heterozygosity decreases at different rates depending on **mating patterns** (bottom left graph) and **population size** (bottom right graph)
- **Self-fertilization** most extreme case of inbreeding → 50% reduction in heterozygosity per generation
- Homozygosity for deleterious recessive alleles results in **inbreeding depression**





Inbreeding depression

- The **reduction in fitness** of **inbred offspring** compared to outcrossed offspring
- Manifested by reductions in viability (survival) and fertility (reproductive output)
- Strong inbreeding depression favours survival of outbred offspring, \therefore **favours outbred mating systems**
- In outbred population, many deleterious genes but sheltered by heterozygosity

Plants and inbreeding

- **Darwin** studied and wrote book about inbreeding/outbreeding in plants \rightarrow compared fitness seeds (offspring) of crossed vs. selfing individuals of hermaphroditic plants
- Most plants **hermaphrodites** \rightarrow how do they avoid inbreeding?
- Darwin studied mechanisms plants evolved to reduce inbreeding:
 - o **Self-incompatibility**: recognize own pollen and rejects it
 - o Also, few plants **dioecious**: separate sexes (sexual selection)
- Some plants can evolve self-fertilization if lack of pollinators
- Ex. *annual* water hyacinth (not clonal)
 - o Brazil populations: mostly outcrossing, visited by long-tongued bees \rightarrow bigger flowers
 - o Jamaica/Cuba populations: largely selfing, long distance dispersal \rightarrow smaller flowers
- **Baker's law**: long distance-dispersal favours selfing forms b/c single individual can start colony w/o mates or pollinators



Large-flowered bee-pollinated outcrosser from Brazil Small-flowered selfer from Jamaica

Fisher: automatic selection of selfing gene

- Selfing genotype: mother *and* father for own seed, also sends out pollen \rightarrow 3 gene copies going forward to next generation
- Outcrosser genotype: only mother for own seed, also sends out pollen \rightarrow 2 gene copies going forward to next generation
- \therefore Selfing should have **transmission advantage**
- So why isn't entire world selfing? \rightarrow b/c about quality, not quantity

	Outcrosser	Selfer
Seed	1	2
Pollen	1	1
Total Gene Copies	2	3

Selfing form has a transmission advantage

Sexual dimorphism

- Arises from sexual selection

- Males concerned with finding mates → evolve big colourful flowers to attract pollinators and pollinate females
- Females concerned with resources → don't need to evolve big flowers

Lecture 18: Population Structure, Gene Flow and Genetic Drift

Geographic differentiation concerned with:

- Variation between populations (as opposed to within)
- Proportion of genetic variability in species from within vs. between populations
- Differentiation due to local adaptation

Fisher-Wright debate

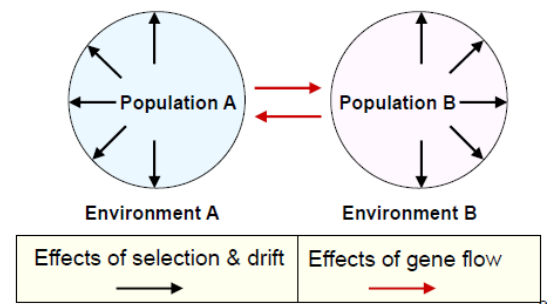
- **Wright**: **population structure** and **genetic drift** important in evolution
- **Fisher**: **natural selection** most important in evolution

Definitions

- **Population**: group of individuals of single species occupying given area at same time
- **Migration**: movement of individuals from one population to another
- **Gene flow**: movement of genes from one population to another

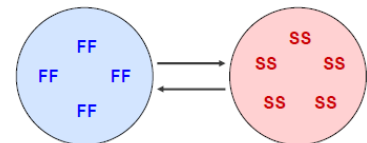
Effects of selection, gene flow and genetic drift on population divergence

- Gene flow = cohesive force
- Selection, genetic drift = diverging force
- Selection and genetic drift cause speciation → two populations of a species become so different that they cannot mate with each other



Measuring gene flow

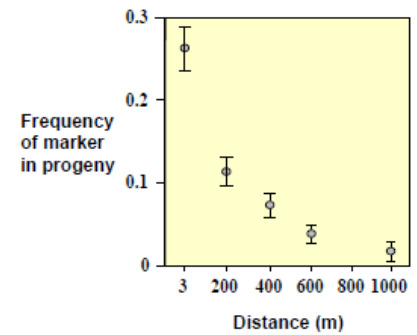
- Difficult to observe and measure
- Distinguish b/w potential (i.e. migration) vs. actual, gamete vs. individual
- Use experimental approaches
- Use neutral **genetic markers** (polymorphic neutral genetic variation used to study population processes affecting genetic diversity)
- Ex. allow two populations **fixed for alternative alleles** to mate, frequency of heterozygous offspring (**FS**) = estimate of gene flow
- Note: gene flow can be **asymmetric** (i.e. more strong in one direction, ex. from dominant wind in one direction)



Gene flow and GMO crops

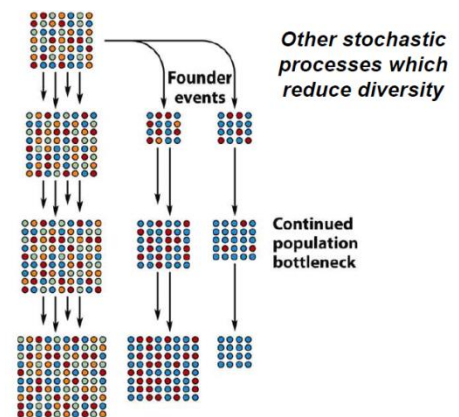
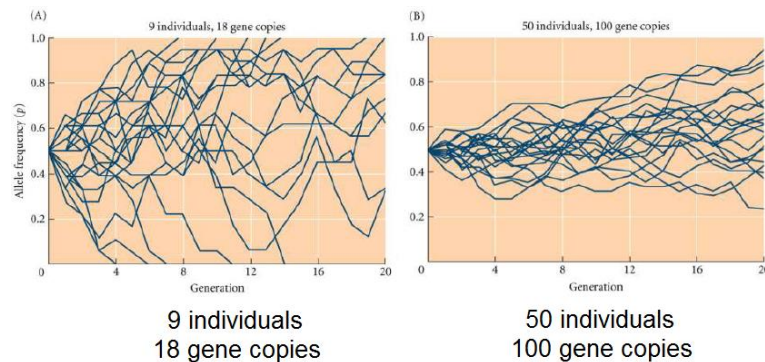
- Many crops have wild relatives they are **inter-fertile** with (ex. rice, oats, canola, carrots)

- **Hybridization** b/w crops and related weeds well documented
- Problem b/c want to conserve genetic diversity of crop relatives, not contaminate them
- Also problem for ppl who grow natural crops → need big enough **isolation distance** from GMO crops
- Ex. gene flow b/w crop and weed sunflowers (graph) → most gene flow occurs over short distance, but small amount occurs as far as 1km
- Risk assessment of escape of crop transgenes into wild relatives:
 - o Proximity of wild relatives
 - o Pollination system (wind vs. animal)
 - o Mating system (selfer vs. outcrosser)
- **High risk:** wild pollinated outcrosser w/ relatives nearby
- **Low risk:** selfer w/ no relatives nearby



Stochastic processes

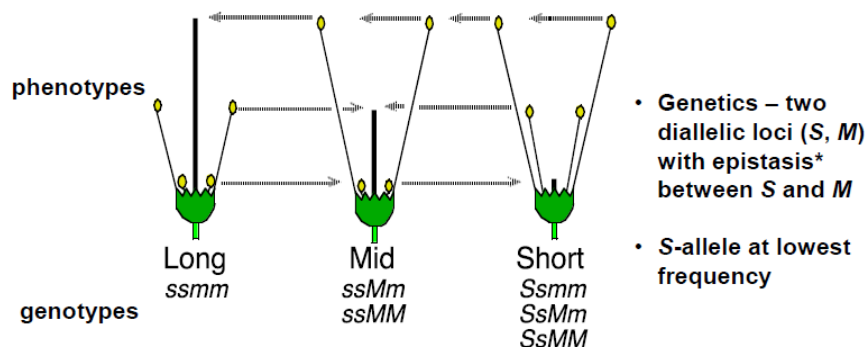
- Unpredictable, random
- Opposite of deterministic (ex. natural selection)
- Include mutations, recombination (↑ diversity)
- Stochastic processes that ↓ diversity:
 - o **Genetic drift:** random fluctuations in allele frequency due to random variation in fecundity and mortality → more evident in small populations (see below)
 - o **Population bottlenecks:** a single sharp reduction in numbers causing loss of diversity
 - o **Founder events:** colonization by a few individuals that start a new population w/ only limited diversity compared w/ source population



Genetic drift and adaptation example: annual water hyacinth

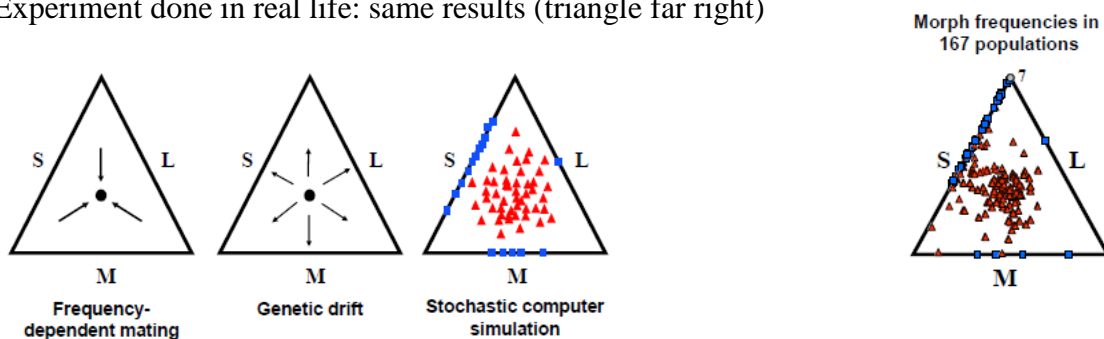
- Genetic drift plays role in evolution of selfing from outcrossing in annual water hyacinth
- **Tristyly** = polymorphism of different lengths of female reproductive organ (style)
- **Disassortative mating:** symmetrical mating system where morphs mate w/ each other, but not w/ themselves; no selfing usually
- Governed by 2 genes (S locus, M locus)
 - o Long = double recessive (s and m), homozygous at both loci
 - o Medium = dominant M locus and recessive s locus
 - o Short = dominant S locus

- Why does S allele dominate genotypes at **diallelic loci**? → epistasis
- **Epistasis**: interaction b/w alleles at different loci affecting phenotype (presence of one allele at genotype affects other genotype)
- Rare morph has fitness advantages → “**frequency dependent selection**”
- Frequency dependent selection leads to **equilibrium morph frequency of 1:1:1**
- ∴ **Polymorphism maintained by frequency-dependent selection**



Effects of frequency-depending mating on morph frequencies in trisyly populations

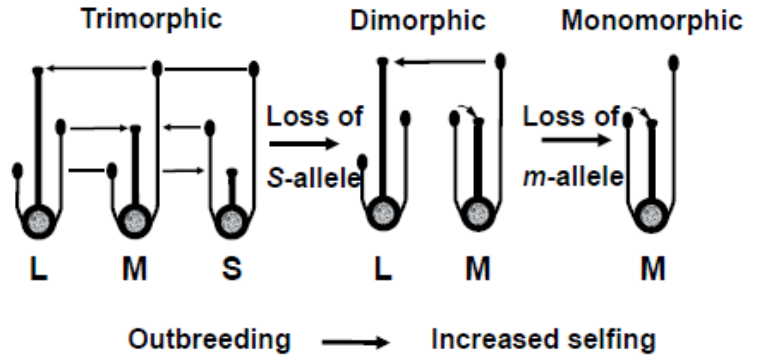
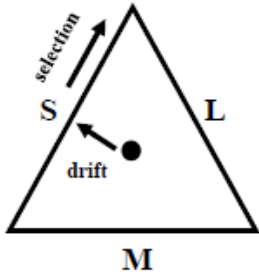
- Frequency-dependent mating drives populations to 1:1:1 frequencies
- Genetic drift drives populations away from 1:1:1 frequencies
- Stochastic computer simulation → subjected to genetic drift at various times
- Computer model shows **asymmetric loss in morph frequencies** → short morph lost most often (Why? Since genetic drift random process, why aren't phenotypes lost equally?)
- Genetic drift makes **low frequency alleles most vulnerable to loss**
 - S allele only found in 1 morph (short) → lowest frequency
 - s, M and m alleles found in all morphs
 - ∴ S allele lost most often → responsible for short morph → short morph lost most often
- Experiment done in real life: same results (triangle far right)



Evolution of selfing through genetic drift and natural selection

- Genetic drift causes ↓ population → inbreeding
- Selection favours selfing b/c small populations do not attract pollinators
- ∴ **Joint action of genetic drift and natural selection results in evolution of selfing from outcrossing**
- ∴ Polymorphism → monomorphism

Model of the breakdown of tristily



Lecture 19: Natural Selection and Adaptation

Co-adaptation example

- Orchid from Madagascar w/ long floral tube pollinated by moth w/ exceptionally long proboscis
- Darwin predicted existence of moth → century later it was discovered
- Example of **co-adaptation**

Definitions

- **Fitness**: relative genetic contribution of individuals to next generation as a result of differences in viability and fertility (=Darwinian fitness)
- **Selective advantage**: some individuals better adapted to environment ∴ have higher fitness
- **Adaptation**: any trait that contributes to fitness by making an organism better able to survive or reproduce in a given environment [noun]; evolutionary process that leads to the origin and maintenance of such traits [verb]

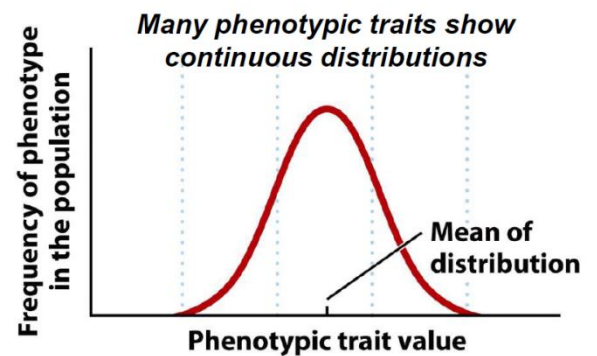
Artificial selection	Natural selection
<ul style="list-style-type: none"> ▪ Domesticated plants and animals; selection experiments in genetics ▪ Selection by humans ▪ Has a purpose or goal 	<ul style="list-style-type: none"> ▪ All organisms ▪ Selection by abiotic and biotic environment ▪ No purpose or goal; simply a blind mechanistic process w/ no foresight

Measuring selection

- **Quantitative traits** (continuous variability)
- Ex. size, number → many genes of small effect influencing trait expression
- Bell shaped curves

Types of selection

1. **Stabilizing selection**
 - No change in mean
 - Change in variance (↓)

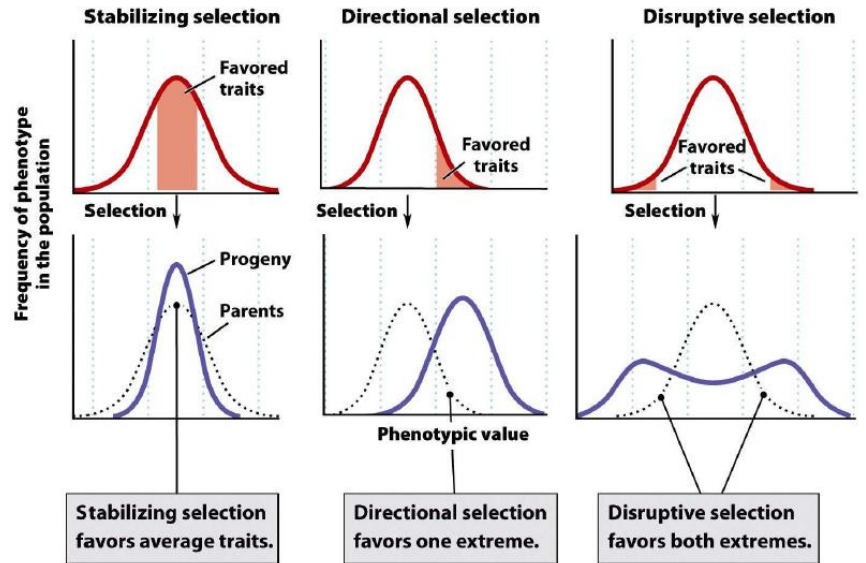


2. **Directional selection**

- Change in mean
- No change in variance
- Usually climate change effects

3. **Disruptive selection**

- Change in mean
- Change in variance
- “Bimodal distribution”
- Can lead to **speciation** if species diverge enough to become reproductively isolated
- Requires **spatial heterogeneity** or **discrete resources**



Stabilizing selection example: mammal birth weight

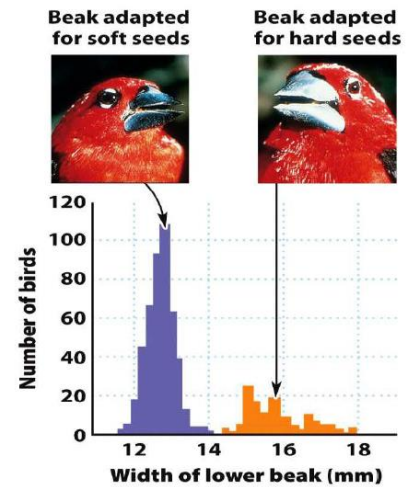
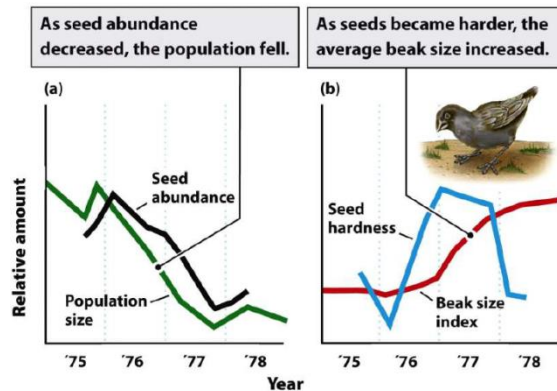
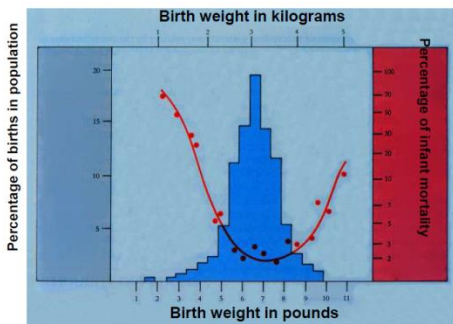
- Small babies too small to survive
- Large babies can kill mother during birth
- Note: think about third world countries for humans, where no medical technology to perform c-sections, etc.

Directional selection example: beak size in Galapagos finches

- Peter & Rosemary Grant’s study on finches
- B/w 1975-78, El Nino event → seeds ↓ = population ↓
- Only hard seeds available → selection for large and tough beaks

Disruptive selection example: beak size in African finches

- Discrete resources → soft and hard seeds
- Different beaks for soft/hard seeds



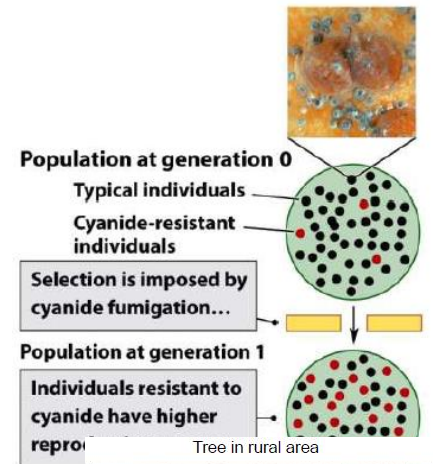
Struggle to determine the mechanisms of selection

- Today hundreds of measurements of selection demonstrating fitness differences and evolutionary change in traits

- Fewer convincing cases that demonstrate mechanisms (agents) of selection in natural populations

Evolution of cyanide resistance

- Scale insects → **standing genetic variation** includes resistance to cyanide
- Alleles conferring cyanide resistance found at **low frequency** in populations
- Resistance spreads through population when selection is imposed by cyanide fumigation
- ∴ **Selection pressure = ↑ frequency of resistance alleles**
- This process serves as model for evolution of many forms of resistance (ex. antibiotics, insecticides, herbicides)



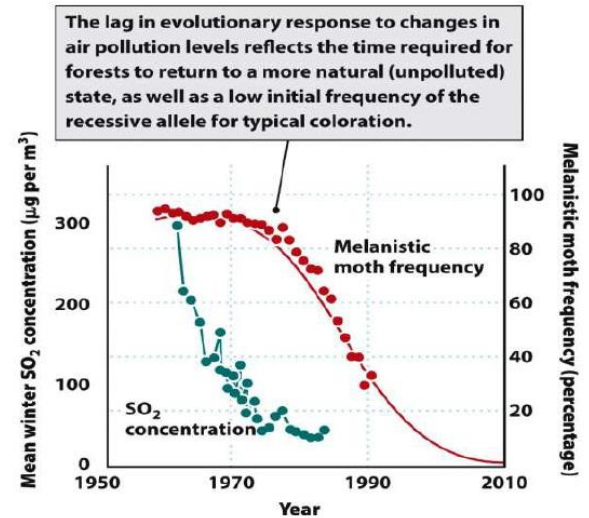
Evolution of industrial melanism in peppered moth

- Light and dark forms of species that rest on trees
- In UK, before 1850 dark moths are rare; caused by **single dominant allele**
- Industrial pollution blackened tree trunks near cities resulting in increase in black form
- **Black variant replaces white in polluted areas**; white form predominates in rural unpolluted areas
- Mechanism of selection thought to be **predation by birds** and **differences in crypsis** (camouflage) depending on background of tree trunks
- **E.B. Ford** recruited **Kettlewell** to investigate bird predation hypothesis
- Observations and experiments in 1950s involving mark and recapture of moths provide support for hypothesis
- His findings thought to provide **first demonstration of mechanism of natural selection in wild**



Doubts raised by Kettlewell's bird predation experiments

- Moths raised in lab → may have influenced behaviour
- Moths put on trunks at unnaturally high densities
- Moths rarely seen on trunks
- Releases conducted during day
- Possibility of bat predation not investigated
- **Majerus** replicated experiments but more carefully → got same results, **Coyne** still doubtful
- Decline in frequency of black (**melanic**) form after introduction of 'Clean Air Act' in UK in 1956 further supports hypothesis (graph)
- Similar experiment by **Hoekstra**: mouse coat colour polymorphism in contrasting habitats maintained by avian predators



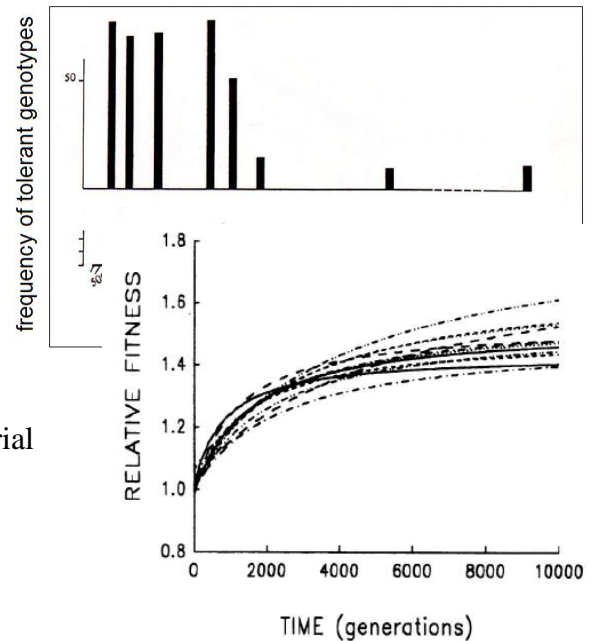
Evolution of heavy metal tolerance in plants (Bradshaw)

- Mine waste heavily polluted w/ heavy metals (ex. Pb, Cu, Ni); most mines < 100 years old
- **Heavy metal tolerant genotypes** occur at low frequency in nearby uncontaminated pastures
- Tolerant genotypes invade mine tailings from nearby pastures
- **Gene flow restricted** b/w pastures and mine b/c of **flowering time differences** → ∴ genes for tolerance maintained on mines (not contaminated)
- Tolerance genes don't spread to pasture b/c no selection for it (no adaptive significance for tolerance on pastures) and energetically costly
- Nontolerant outcompetes tolerant on normal soil b/c no energy diverted to metal tolerance mechanisms
- Heavy metal tolerance in plants has evolved independently in many geographical areas

Experimental evolution (Lenski)

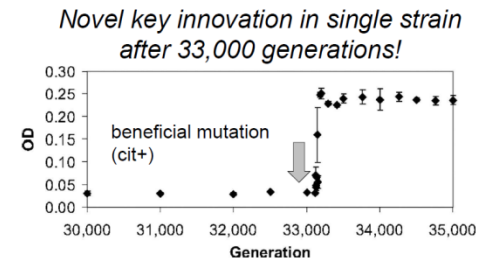
- 20 year experiment w/ *E. coli* (picked *E. coli* b/c evolves fast → "witness evolution")
- 12 populations propagated → 42,000 generations in serial culture
- Freeze sample of *E. coli* every generation to compare relative fitness
- Measure of fitness = growth rate of colony
- First graph
 - All populations rapidly increased in fitness
 - Similar adaptations across strains (ex. larger cell sizes, higher maximum growth rates on glucose)

Evolution of zinc tolerance in grasses



Samples frozen at intervals allowing relative fitness of different generations to be compared

- Parallel mutations at same genes
- Some unique adaptations and distinct genetic changes
- Second graph
 - OD = optical density, measure of number of bacteria (shine light through medium)
 - Beneficial mutation fixes → growth rate ↑ significantly



Open questions about adaptation

- What is the relative importance of **standing genetic variation** (variation already present in a population) vs. **new mutations**?
- Are **convergent adaptations** in unrelated organisms the result of the same or different genes?

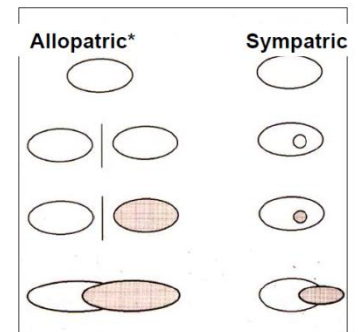
Lecture 20: Species, Speciation and Hybridization

Species definition

- **Taxonomic (morphological) concept**: based primarily on distinct morphological differences
- Problem w/ taxonomic concept is lack of objectivity → arbitrary definitions
- **Biological concept (Mayr)**: based on inter-fertility (crossability) among individuals
- Problem w/ biological concept is unpractical to test inter-fertility of all organisms
- In evolutionary biology, use biological species concept
- No universal species concept

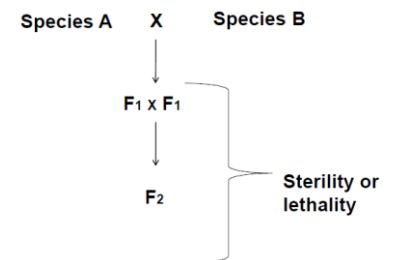
Modes of speciation

- **Allopatric**: population separated by geographical barrier → differential adaptation → reproductive isolation
- **Sympatric**: subpopulation within population evolves reproductive isolation (common in plants)
- *Sympatric speciation controversial b/c gene flow should prevent reproductive isolation (whereas in allopatric speciation geographical barrier impedes gene flow)
- **Reproductive isolation** when two populations come into **secondary contact** and can't interbreed



Reproductive isolation

- Speciation involves evolution of reproductive isolation b/w populations (biological concept)
- When genetic differentiation occurs b/w populations and they are **no longer inter-fertile**
- Can occur at many stages: finding a compatible mate; mating and fertilization; development of zygote; adult growth and survival; reproduction and fertility of offspring
- **Premating (prezygotic) isolation**: preventing zygote formation
 - o Geographical, ecological (species occur in different locations)
 - o Temporal (species mate at different times)
 - o Behavioural (species have different behaviours to attract mates)
 - o Mechanical, prevention of gamete fusion
- **Postmating (postzygotic) isolation**: preventing proper functioning of zygotes once formed
 - o **Intrinsic**: genetic problem, independent of environment (ex. sterility, lethality)
 - o **Extrinsic**: dependent of environment, taken out by selection (ex. inviability, abnormal development)



Premating isolation example: apple maggot flies

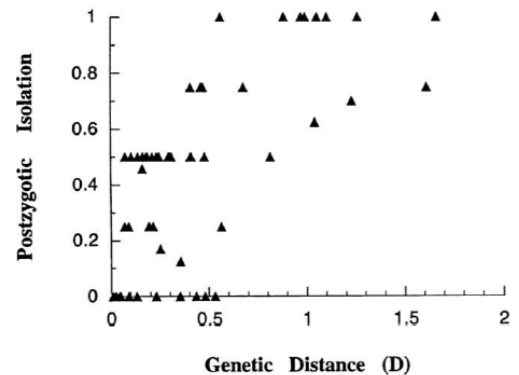
- After introduction of apple trees, subpopulation of flies switched from hawthorn trees → apple trees
- Reproductive isolation caused by **temporal mechanism**: different times of fly emergence correspond with apple tree flowering
- **Differences in host plant emergence and mating on preferred host restricts hybridization**
- This reduces gene flow in **sympatry** (same region) ≈ 6%

Premating isolation example: monkey flower (Shemske)

- Two closely related species: one pollinated by hummingbirds, one pollinated by bees → isolated b/c **different pollinators**
- Also isolated by different environments (different altitudes) → **geographical mechanism**
- Note: species don't hybridize in wild, but if brought into lab they can → shows they are very genetically similar

Intrinsic postmating isolation example: fruit flies (Coyne and Orr)

- Studied relation b/w **genetic distance** and **postmating isolation** → looked at dozens of different species of fruit flies
- Genetic distance = measure of degree of genetic differentiation
- Idea was the more genetically different flies are, the less likely they are to produce fertile offspring
- ↑ **genetic differentiation = more likely to be reproductively isolated**
- Plot can be viewed as time course for evolution of reproductive isolation

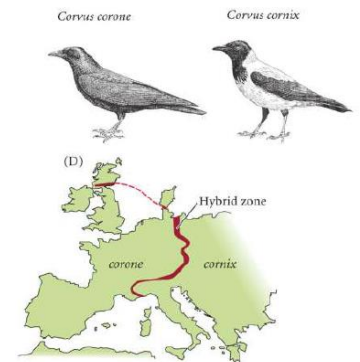


Intrinsic postmating isolation example: mule

- Mule is **sterile** hybrid from cross b/w male donkey and female horse

Extrinsic postmating isolation example: European crows

- Carrion crows west, hooded crows east
- Hybridize occasionally in zone where habitats meet, but **hybrids very poorly adapted** and don't survive
- Species largely allopatric, gene flow not pervasive

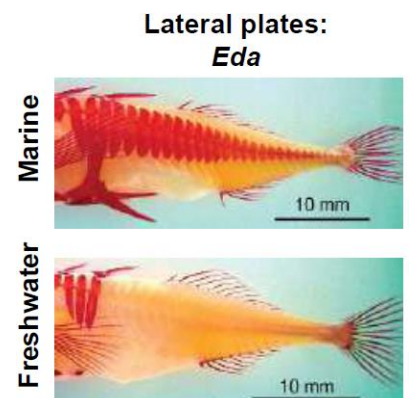


Adaptation and speciation

- In many cases, evolution of local adaptation as result of divergent selection leads to reproductive isolation and speciation
- Commonly referred to as "**ecological speciation**"
- Much current research focuses on determining mechanism of selection and identifying "**speciation genes**"

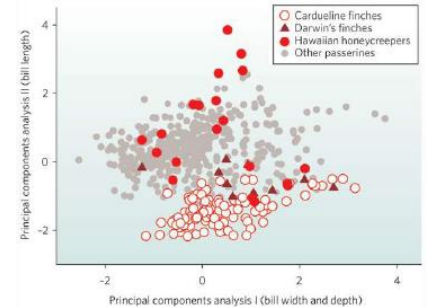
Adaptation and speciation example: stickleback fish (Schluter)

- Marine environments: bony armour favoured as **protects against large fish predation**
- Freshwater environments: loss of plates favoured as **increases growth rate**, helping fish breed earlier and survive winter (lakes freeze, oceans do not)
- Gene controlling lateral plates = "**Eda**"



Adaptive radiation

- Evolution of **ecological and phenotypic diversity** within a rapidly multiplying lineage as a **result of speciation**
- From a single common ancestor the process results in an array of species that differ in traits allowing exploitation of a range of habitats and resources
- Characterized by:
 1. **Recent common ancestry from single species**
 2. **Phenotype-environment correlation**
 3. **Trait utility**
 4. **Rapid speciation**
- Ex. Hawaiian honeycreepers → variation in beak morphology



Causes of adaptive radiation

- 1) **Ecological opportunity**: abundant resources and few competitors, often occur on oceanic islands or aquatic counterparts (ex. African rift lakes)
- 2) **High rates of speciation**: some species have higher capacity for speciation than others, can examine mainland clade (ex. Darwin's finches and Hawaiian honeycreepers also radiated on mainland, whereas Galapagos mockingbirds have not radiated on islands or continents)
- 3) **Origin of key innovation**: mutation allowing organism to exploit environment (ex. toepad in island Anoles lizards, not present in mainland; floral nectar spur in Columbine flowers)

Hybridization

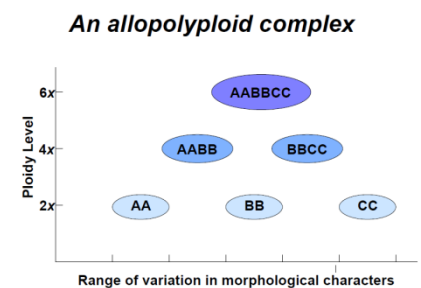
- **Exchange of genes** b/w species as a result of occasional inter-specific mating
- *Gene flow can occur at low levels w/o violating biological species concept → recognize that **fertility/sterility is a continuum**
- Varies among different groups of organisms → common in plants and fish, rare in mammals
- Can result in complex patterns of variation
- Variation can be of evolutionary significance resulting in speciation, especially by polyploidy

Polyploidy

- Organism, tissue or cell w/ more than two complete sets of homologous chromosomes
- "Unreduced genes" → gametes have same # genes as somatic cells
- **Autopolyploidy** (ex. AAAA)
- **Allopolyploidy** (ex. AABB) → arises from occasional hybridization b/w species, most common type
- Odd # genes = sterile → imbalance of chromosomes (ex. triploid)
- Even # genes = fertile (ex. diploid, tetraploid, hexaploid)
- Evolutionary significance:

1. Polyploids reproductively isolated from parents ∴ **new form of sympatric speciation**
2. Polyploids exhibit **novel phenotypes allowing exploitation** of new habitats
3. **Hybrid vigour** due to heterozygosity (particularly allopolyploids) → benefit of several genotypes
4. Appx. **1/2 of all flowering plants of polyploidy origin**, including many crop plants and invasive species

- **Abbott**: studied hybridization of diploid and tetraploid *Senecio* flower species



Lecture 21: Phylogenetics and Macroevolution

Biological classification

- **Linnaeus** = “father of taxonomy,” invented hierarchical system of classification (binomial nomenclature)
- Biological classification enables interpretation of origins and evolutionary history
- **Taxon**: a named taxonomic unit at any level (ex. kingdom, phyla, etc.)
- **Taxonomy**: the theory and practice of classification
- **Systematics**: the study of biodiversity and the evolutionary relationships among organisms

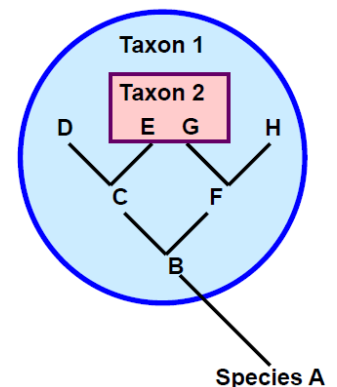
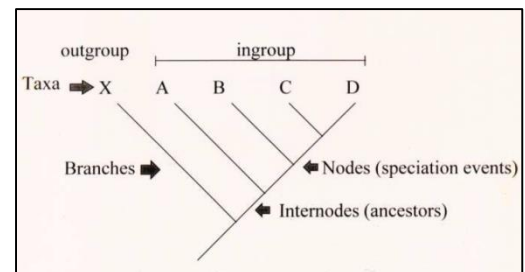
kingdoms
 phyla
 classes
 orders
 families
 genera
 species

Schools of taxonomy

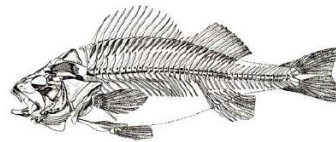
Phenetics	Cladistics
<ul style="list-style-type: none"> ▪ Classifying species based solely on overall resemblance ▪ Treat all characters as equal ▪ Morphological measurements put into computer to generate trees ▪ “Numerical taxonomy” 	<ul style="list-style-type: none"> ▪ Classifying species on the basis of phylogenetic relationships ▪ Founder: Hennig

Phylogenetic trees

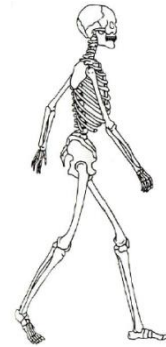
- Depict evolutionary relationships among groups of organisms
- Are hypotheses about evolutionary history
- **Monophyletic group**: single ancestor gave rise to all species in that taxon and no species in any other taxon
- **Non-monophyletic group**: a taxon whose members are derived from two or more ancestral forms not common to all members
- **Clade**: all taxa derived from immediate common ancestor
- Monophyletic classifications preferred
- In diagram, taxon 1 = monophyletic and constitutes a clade
- In diagram, taxon 1 = nonmonophyletic
- **Ancestral trait**: trait shared w/ common ancestor
- **Derived trait**: trait that differs from ancestral trait in lineage
- **Homology**: similarity of traits due to shared ancestry
- **Homoplasy**: similarity of traits due to convergent evolution



- Why phenetics died out? B/c resemblance of traits could be due to shared ancestry or convergent evolution → ∴ classification does not predict evolutionary relationship
- Ex. human and fish skeleton are homologous structures



Fish Skeleton

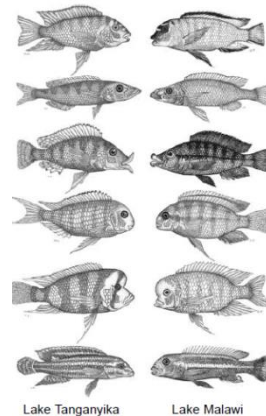


Human Skeleton

one

Convergent evolution

- Evolution of structures that resemble another and perform similar functional roles due to shared ecology of unrelated organisms
- Ex. **convergent evolution of desert plants**
 - o Succulence (absorbent/fleshy tissue) → store water
 - o Spiny growth form → deter herbivory b/c succulence attracts herbivores
- Ex. **convergent evolution of cichlid fish** in African Great lakes
 - o Independent evolutionary radiations in two lakes
 - o Same forms → similar feeding strategies

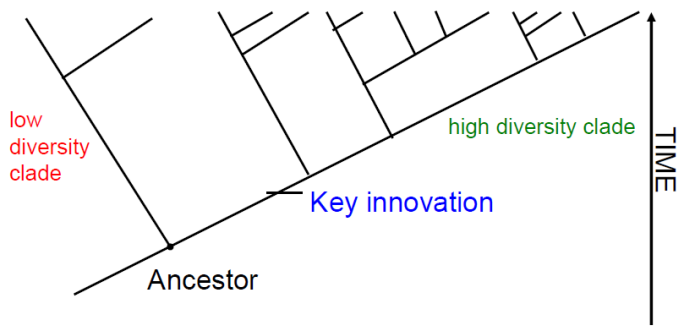


Molecular biology and phylogeny reconstruction

- All life related through **branching descent**
- **Common genetic code** is evidence that all life is related
- Evolutionary relationships among species reflected in their DNA and proteins
- Genes or parts of a gene can be sequenced for different species
- Species can be assessed for changes in sequence of nucleotides
- These changes can be used to construct relationships in branching diagram (phylogeny)
- DNA sequencing enables rapid reconstruction of **tree of life** (Wayne & David Maddison)

Key innovations

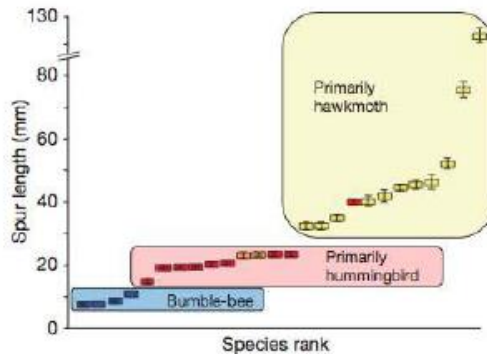
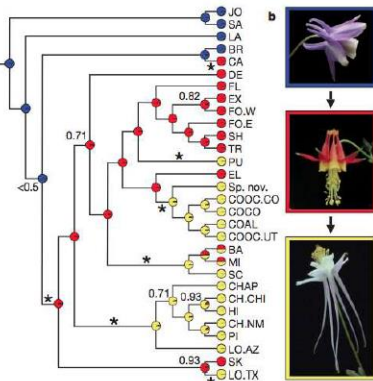
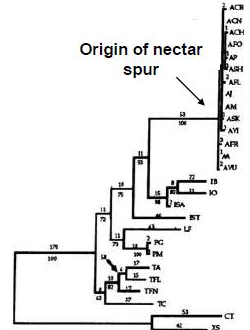
- Origin of a novel trait resulting in adaptive radiation
- Carriers of the trait can exploit new resources or sets of habitats
- Usually associated w/ rapid evolutionary diversification (i.e. adaptive radiations)
- Phylogenies used to understand origin and evolution of traits



**Key innovation example:
nectar spurs in columbine**

flowers

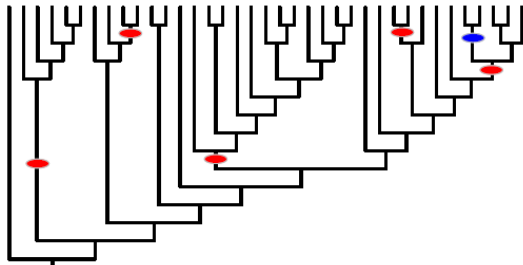
- Phylogeny shows **rapid burst of speciation w/ acquisition of nectar spur** → short branch lengths in comparison with sister group
- 16 fold variation in nectar spur length among species
- From phylogeny, **clear directionality in spur length evolution** (evolving longer), no evidence of reversal to shorter spurs
- Pollinators w/ diff length mouthparts can feed from flowers w/ diff length spurs
- 7 independent pollinator shifts → 2 from bee to bird, 5 from bird to hawkmoth
- **Pollinator shifts** associated w/ speciation events due to pre-mating isolation
- ∴ Key innovation allows lineage to diverge and adapt to different pollinators



Key innovation example: sexual conflict in water striders

- **Sexual conflict**: when interests of males diff than interests of females
- **Bateman's principle**: factors affecting male and female fitness are different
- Males → fitness limited by access to females (reproductive cost low)
- Females → fitness limited by resources (reproductive cost high)
- In water striders, optimal mating rate is lower for females than males → female stores sperm, mating has costs for female (ex. parental care subjects females to predation)
- Females tend to resist most mating attempts by males
- **Males evolved grasping structures (armaments) to overcome resistance**
- **Females evolved behaviours to aid in resistance**
- Antagonistic coevolution → arms race
- Arms race predicts evolution of armaments over evolutionary time → shows up as preponderance of gains on phylogeny

Evolution of antennal armaments in *Rheumatobates*.



	Gains	Losses
Antennae	5	1
Forelegs	5	2
Mid legs	3	2
Rear legs	4	2
Total	17	7



Gains of male armaments are much more common, suggesting an arms race over evolutionary time.

Lecture 22: Contemporary Evolution and Invasive Species

Invasive species examples

- **Lantana camara invasion in India threatens tigers:** distinctive smell from flower rubs onto tigers fur → repels mates → tiger population ↓ = tourist economy ↓
- **Cane toad invasion in Australia threatens reptiles:** successful at controlling cane beetles devastating sugar cane crops in Puerto Rico and Hawaii; not successful in Australia and multiplied prolifically reducing biodiversity, especially reptiles
- **Nile perch invasion in African lakes threatens cichlid fish:** Nile perch introduced w/ intention to eat → extinction of endemic cichlid fish species
- **Asian carp invasion of Great Lakes:** introduced to North America w/ intention to eat, travelling north → worried about invasion in Great Lakes

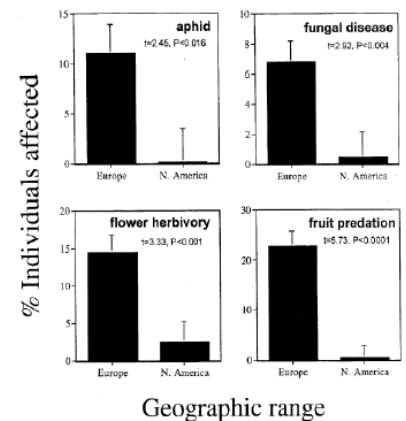
Biological invasions

- Successful establishment of a species in a region not previously occupied followed by rapid range expansion
- Do not always involve harmful species, but most do
- **Native:** indigenous species that occurs wild in a given region
- **Alien:** species that has been introduced to a part of the world to which it is not native (also referred to as adventive, exotic or introduced species)
- **Negative consequences:**
 - Disrupt ecological processes in natural plant and animal communities
 - Displace native species leading to their extinction
 - Adverse effects on human health
 - Serious economic and social impacts through reduction of yields in agriculture and fisheries
- Invasive species thrive in disturbed sites: ↑ **disturbance = more vulnerable to invasion**
- Disturbance can be anthropogenic (ex. logging) or natural (ex. volcanic eruption)
- Ex. pampas grass invasion along abandoned fire trail → pampas grass only grows where land disturbed



Enemy release hypothesis example: white campion flowers (Wolfe)

- Wolfe studied **differences in enemy attack** in populations of white campion from Europe (native range) and North America (alien range)
- Pest and disease pressure 17x higher in native range compared to alien range, involved both specialists and generalists → seed and fruit predation, aphids, snails, florivory
- Ex. of **enemy release hypothesis:** introducing species to alien range “releases” from biological regulators ∴ allowing species to thrive
- Without enemies such as pests and diseases, no ecological balance



Characteristics of successful invasive species

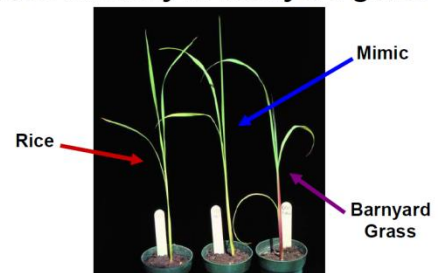
1. Rapid development to reproduction
2. High reproductive output
3. Well-developed dispersal mechanisms
4. Broad ecological tolerance
5. High **phenotypic plasticity** → ability of a genotype to alter its phenotype in response to environmental change (important trait in unpredictable environments)

*Animals usually have lower plasticity compared to plants b/c mobility serves same function

Invasive species and agriculture example: rice mimicry in barnyard grasses

- Weed removal involves ability to distinguish visually b/w crop and weed
- Weeds that look more like crop escape detection inadvertently **selecting for mimicry**
- Selection pressure in barnyard grasses selects for:
 - o Green rather than red colouration
 - o Upright leaves
 - o Same flowering time as rice crops

Rice mimicry in barnyard grass

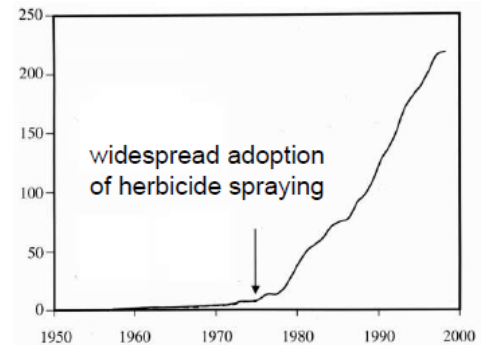


Invasive species and agriculture example: herbicide resistance

- Rapid evolution of herbicide resistant weeds in agriculture
- Now over 300 invasive species that evolved herbicide resistance

Local invasive species example: zebra mussels

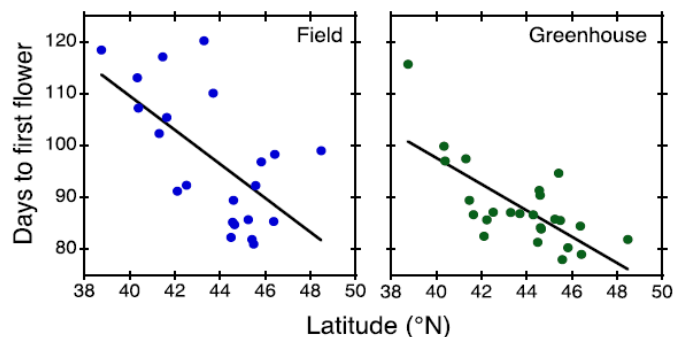
- Arrived in late 80s in ballast water of ocean freighters
- Now abundant throughout Great Lakes
- Single female can produce up to 1 million eggs per season
- Free swimming larvae easily dispersed in water
- Extensive damage to water intake pipes and commercial/sport fisheries
- Source of avian botulism → death of many birds
- Filter feeders → increased water quality (only plus)



Local invasive species example: purple loosestrife

- Aquatic perennial w/ showy purple flowers native to Europe, used as ornamental
- Multiple introductions to eastern N. America during past century followed by invasions of wetlands → moving north
- Characteristics that make purple loosestrife good invader:
 - o **Competitive**
 - o **High phenotypic plasticity**
 - o Produce **millions of small, easily dispersed seeds** w/ high viability
 - o **High genetic variability b/c multiple introductions, outbreeding and polyploidy** → provides opportunities for local adaptation
- Question: is there evidence for rapid adaptive evolution in invasive populations of purple loosestrife?

- **Common garden experiment:** grow samples of purple loosestrife from diff latitudes in a “common garden” → since same environment, any phenotypic differences observed are from genetics
- Results: **flowering time correlated w/ latitudinal gradient of seasonality**
- Indicates **significant genetic differentiation** among populations
- Variation forms a **cline** (a gradual change in trait means over a geographical transect) in time to flowering → northern populations flower faster than southern populations b/c maladaptive to flower late in colder climates
- ∴ Populations farther north have adapted to shorter growing season
- ∴ **Direct evidence of climatic adaptation over contemporary time scale**



Aquatic plant invasion in tropics

- World’s worst aquatic invaders = **water hyacinth** and **kariba weed**
- Kariba weed is pentaploid (5 sets of chromosomes) ∴ sterile, but doesn’t need sex b/c very good at clonal propagation → can outcompete water hyacinth
- Both native to S. America, introduced by humans to Old World tropics
- Both free-floating w/ **prolific clonal propagation**, populations **genetically uniform** and invasiveness due to **high phenotypic plasticity** (NOT genetic diversity)
- ∴ Good invasive species b/c good at cloning and high plasticity, not b/c it adapts
- Herbicide control causes pollution of aquatic habitats so biological control methods used

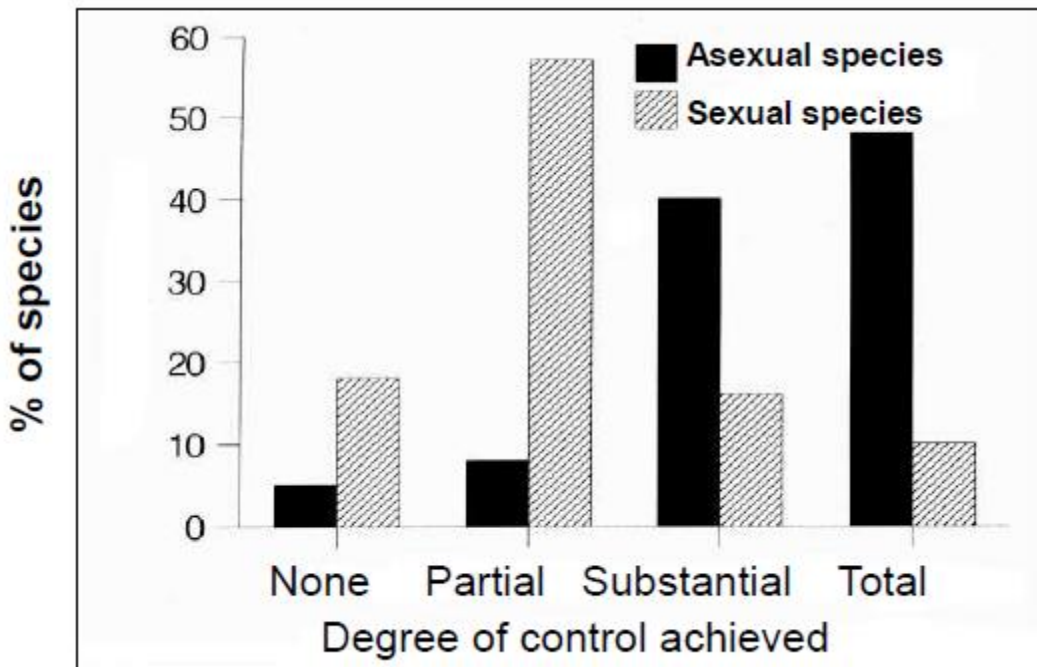
Management of invasive species

- Mechanical – ex. hand weeding, machines
- Chemical – ex. herbicides
- Ecological – ex. burning, flooding
- **Biological control**

Biological control

- The **planned introduction of natural enemies** (ex. predators, parasites, pathogens) to control unwanted populations of invaders in alien range
- Advantages:
 - Non-toxic to humans; if conducted carefully no serious environmental impacts
 - If successful, effects are permanent
 - Economically cheap (chemical control costs 5x more)
- Dangers:
 - Sloppy science creates new invasion

- To **make sure pest is host-specific**, usually “cafeteria experiments” conducted first → pest put in environment w/ invasive species and several domestic crops (ex. rice, wheat) to confirm pest eats only invasive and not crops
- **Asexual species easier to control than sexual species** → b/c asexual has ↓ genetic diversity
∴ less likely to evolve resistance

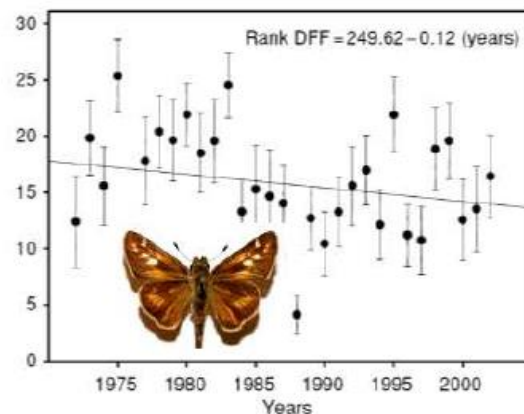
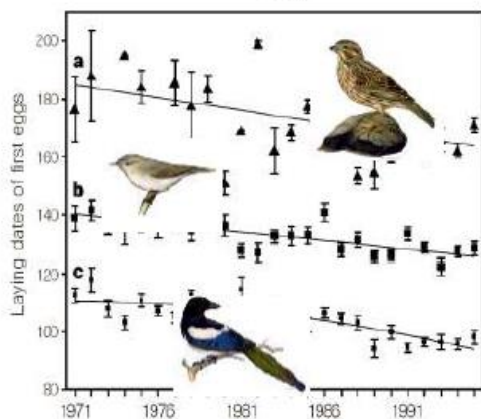
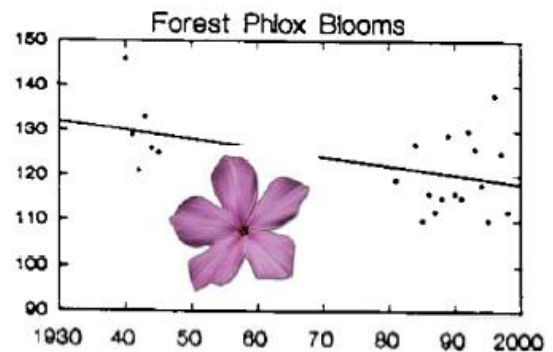
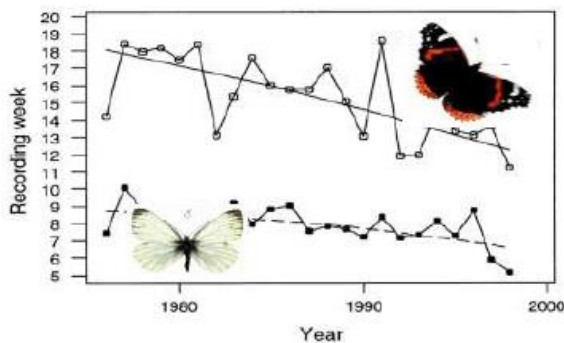
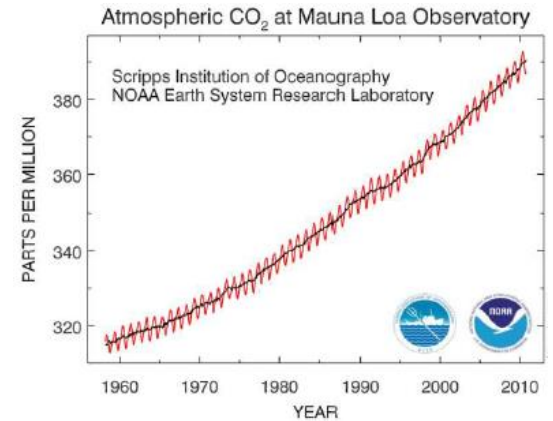


Lecture 23: Biodiversity, Extinction and Evolutionary Biology

Wilson: founder of biodiversity science

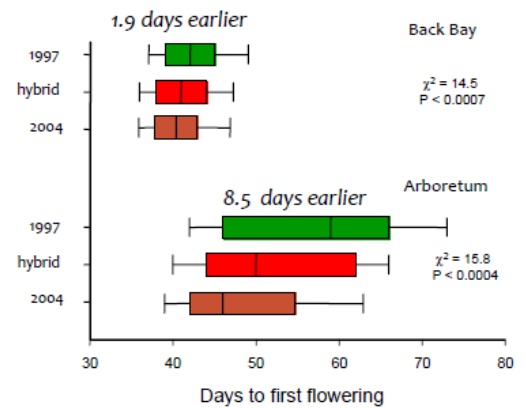
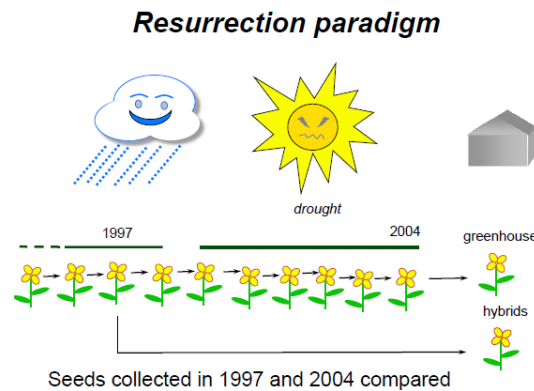
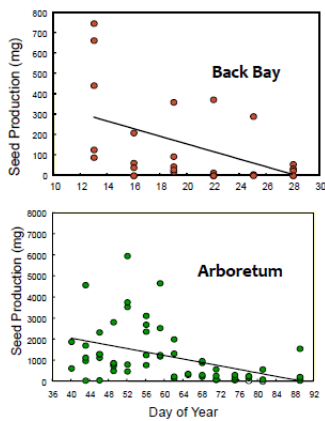
Global warming and climate change

- **Keeling:** longest direct measurements of CO₂ in atmosphere (graph on right)
- Increase in CO₂ as a result of burning of fossil fuels
- Organism **response to climate change:**
 - o **Migrate** to more favourable environmental conditions (ecology)
 - o **Adapt** to changing environmental conditions (evolution)
 - o Go locally or globally **extinct** (evolution)
- Climate change alters phenology, but how much of this response is evolution? (4 graphs below)
 - o **Declining trend** in various parameters (ex. emergence time, flowering time, etc.)
 - o Lines consistent with directional selection, but need studies to confirm not plasticity



Genetic evidence of response to climate change example: field mustard (Weis)

- Studied how drought affected selection of flowering time
- First measured selection by comparing seed production of early vs. late flowering plants → **evidence for directional selection for early flowering** in both populations in 2002 → earlier flowering plants set more seed than later flowering plants (graphs left)
- Then compared seeds collected from 1997 (wet) and 2004 (drought), crossed → hybrids
- Result was **plants flowered earlier** (graph right)
- Occurring b/c genetic variation in populations
- ∴ **Evolutionary response to drought** involves selection for earlier flowering
- *Field mustard has annual life cycle, such responses would take much longer in perennials



Biodiversity

- The number and kinds of living organisms in a given area
- **Interspecific variation** – i.e. species diversity (studied by ecologists)
- **Intraspecific variation** – i.e. genetic diversity (studied by geneticists)
- Biological diversity has many components: species diversity, ecological (functional) diversity, genetic diversity, phylogenetic diversity

Extinction

- The permanent elimination of a species
- Extinction is a normal evolutionary process; 99% of all species that have ever lived are now extinct → extinction is natural, but its current rate is not!
- During past century massive **habitat destruction**, particularly in tropic regions, has increased rates of extinction
- Studies of the causes of extinction require demographic and genetic investigations on the causes of rarity
- Types of extinction
 1. **Background extinction**: turnover of species at a low rate; a natural feature of ecosystems; estimated at ~1 species/yr
 2. **Mass extinction**: very large numbers of extinctions due to natural catastrophes
 3. **Anthropogenic extinction**: caused by humans, estimated at 4-6000 species/yr
- Major causes of species extinction today: habitat destruction (most important); overexploitation of species (ex. overfishing); introduction of pests, predators and competitors

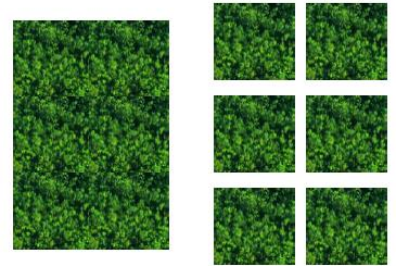
Conservation biology

- The study of those species, ecological communities and ecosystems that are being **negatively affected by human activities**
- Provides the biological concepts and tools for preserving biodiversity and ecosystem function
- Core in ecological and genetic framework, but multidisciplinary (ex. planning, economy, human culture)

Ecological issues in conservation biology

Community level studies

- **Habitat preservation** and **maintenance of species diversity**
- **Application of island biogeographic theory** to design of nature reserves → b/c nature reserves are similar to islands in that they are surrounded by inhospitable land
- **SLOSS**: single large or several small → single large better for biodiversity conservation
- Building of corridors can make several small fragmentations more similar to single large (ex. waterways, “green” passages)



Single large or Several small

Individual species studies

- **Effects of habitat fragmentation** on population ecology and demography → some species need more space than others (ex. elephants vs. orchids)
- Ex. habitat fragmentation of Atlantic coastal forest in Brazil during past 60 yrs threatens endemic golden lion tamarin
- **Keystone species** → some species more important in a community b/c affect all other species, affect structure and function of environment
- Ex. beavers, fig trees, nitrifying bacteria
- **Minimum viable population size**
 - o The number of individuals necessary for a species to maintain or increase its number in a region
 - o The smallest population of a species that can sustain itself in the face of environmental variation
 - o No single number for all species; will vary (ex. cats higher than orchids)

Genetic issues in conservation biology

- **Maintenance of genetic diversity** in rare and endangered species
- Relation b/w heterozygosity and fitness (usually ↓ **heterozygosity** = ↓ **fitness**)
- Preventing inbreeding and inbreeding depression
- Reducing the stochastic loss of genetic diversity from small populations
- **Genetic consequences of small population size**: mating among relatives
 - o Loss of heterozygosity
 - o Inbreeding depression
 - o Fixation of deleterious genes
- Inbreeding in zoos is usually a problem: usually small number of founding individuals
- Strategies for reducing inbreeding depression in small populations needed (ex. genetic testing to determine least related individuals to breed, inseminating w/ wild individual's semen, etc.)
- **Vavilov**: Russian crop geneticist and founder of crop genetic resource conservation

Small population size example: cheetahs

- Restricted to two wild population in southern & eastern Africa
- Survey of 52 enzyme loci indicated complete monomorphism; other cats have 8-21% of loci polymorphic
- Have high juvenile mortality and low spermatozoal counts → suggests inbreeding depression in species as a whole
- Has been proposed that low genetic variation results from historical bottleneck in population size