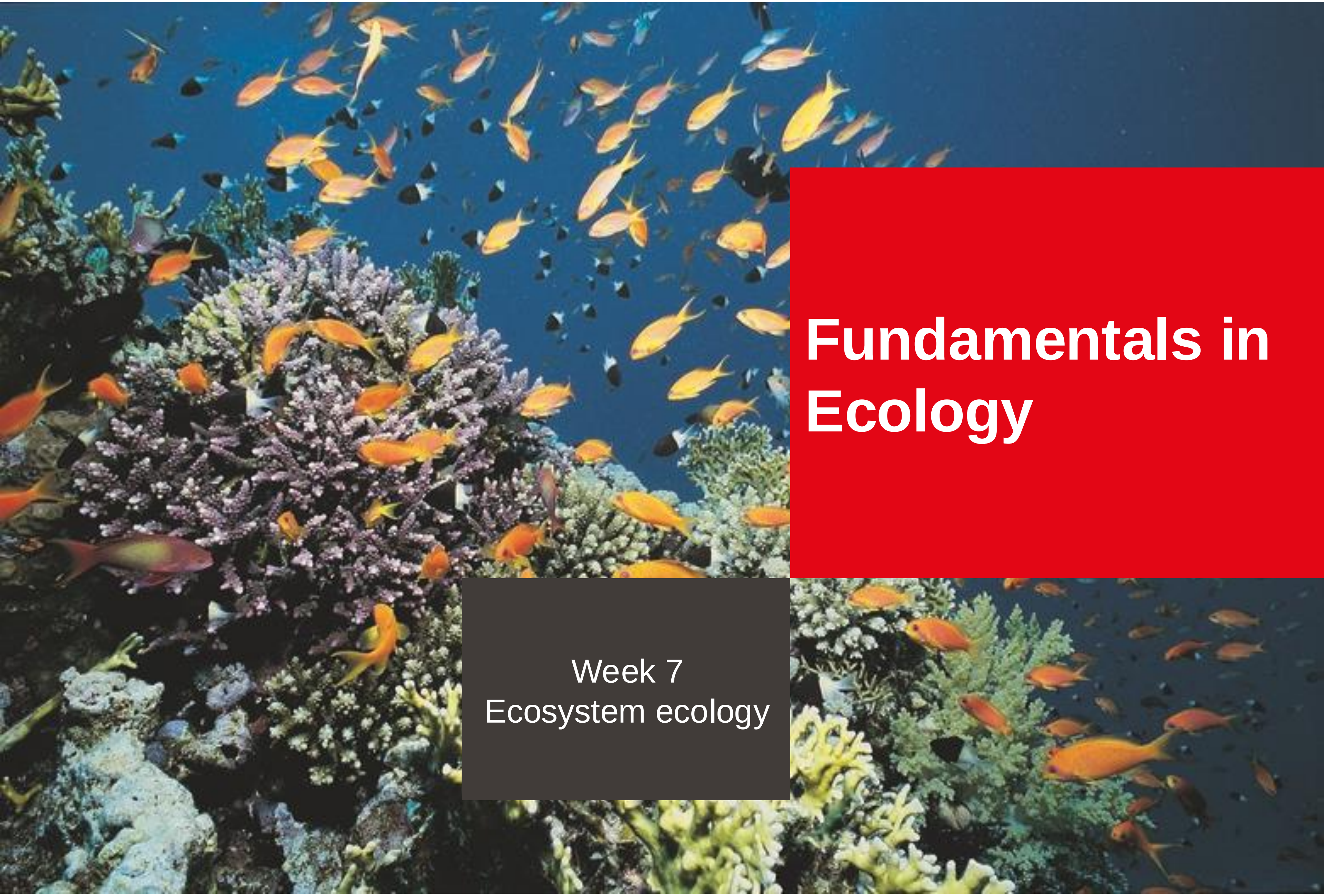
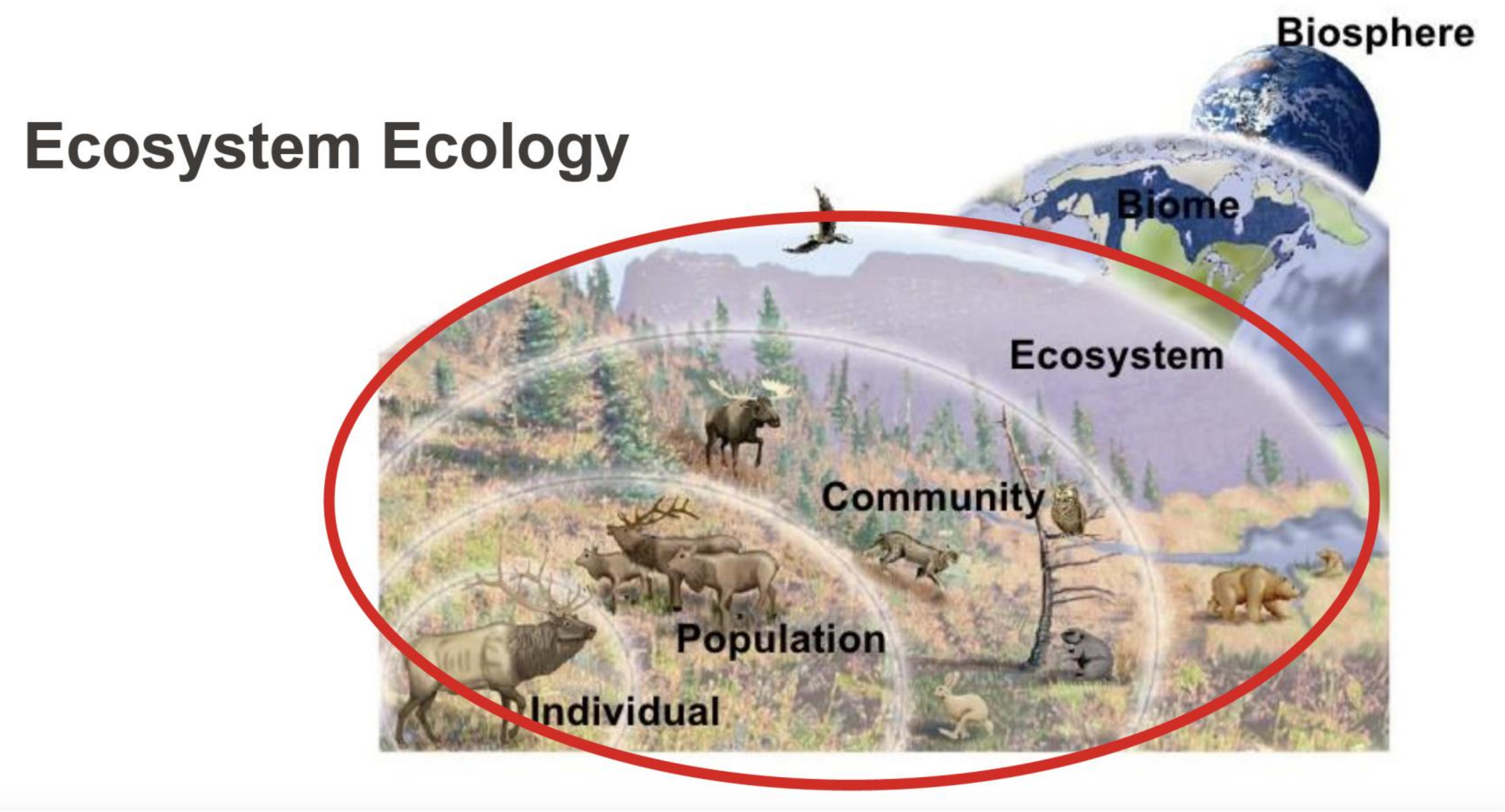


Fundamentals in Ecology

Week 7
Ecosystem ecology

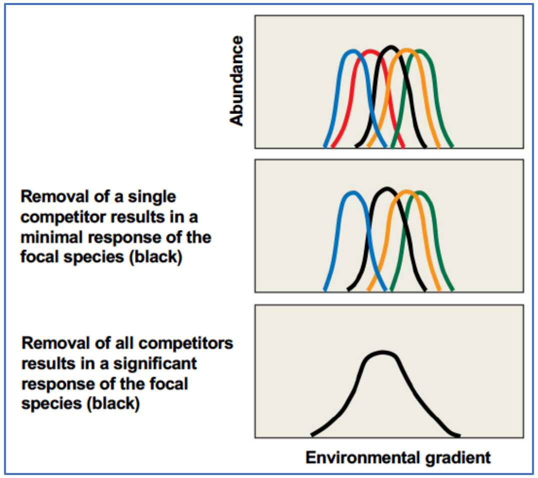
EPFL

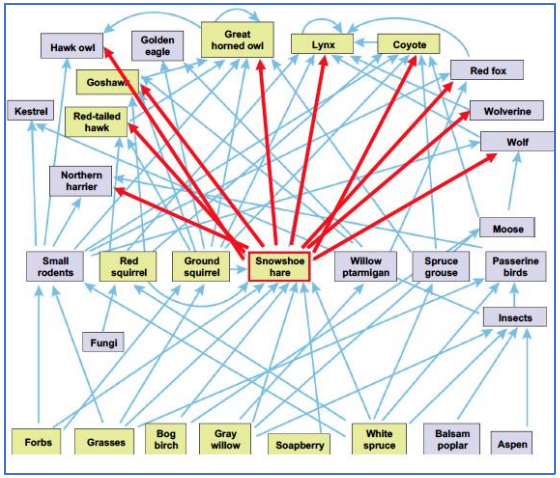


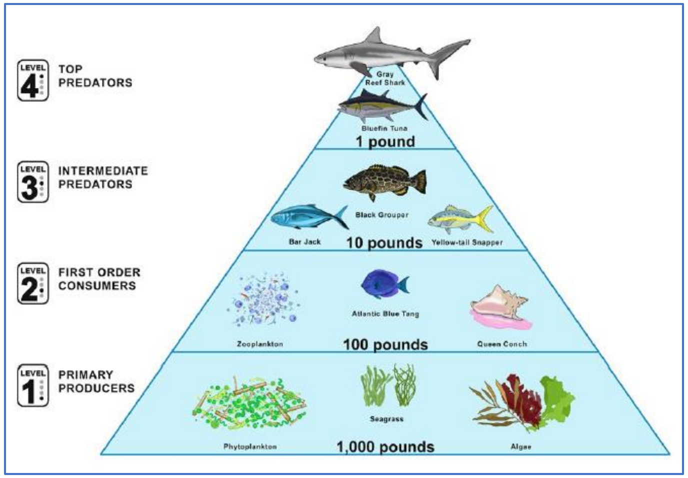
What you have seen over the last weeks

What you have seen over the last weeks:

- Physiology and adaptations
- Population ecology
- Community ecology



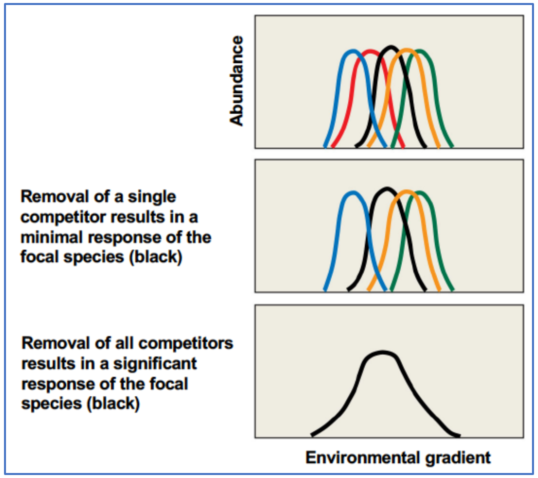


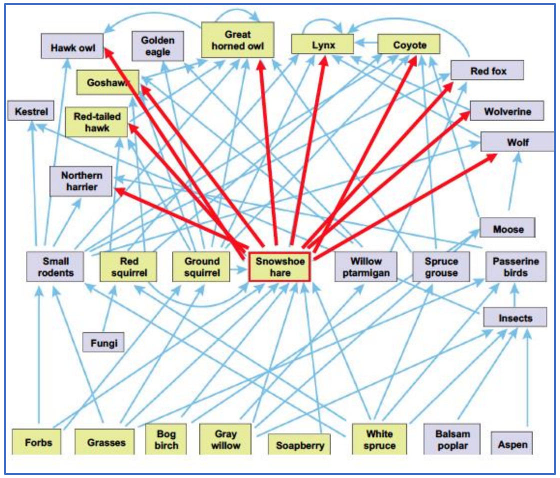


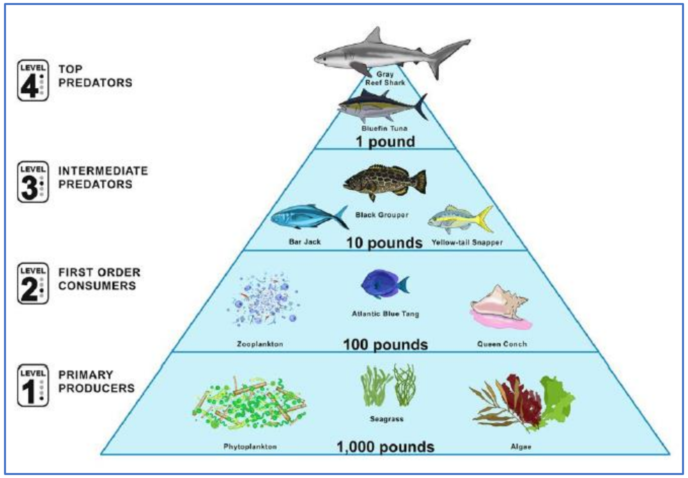
EPFL

What you have seen over the last weeks

Interactions involve fluxes of energy and matter.
This is at the heart of ecosystem ecology.







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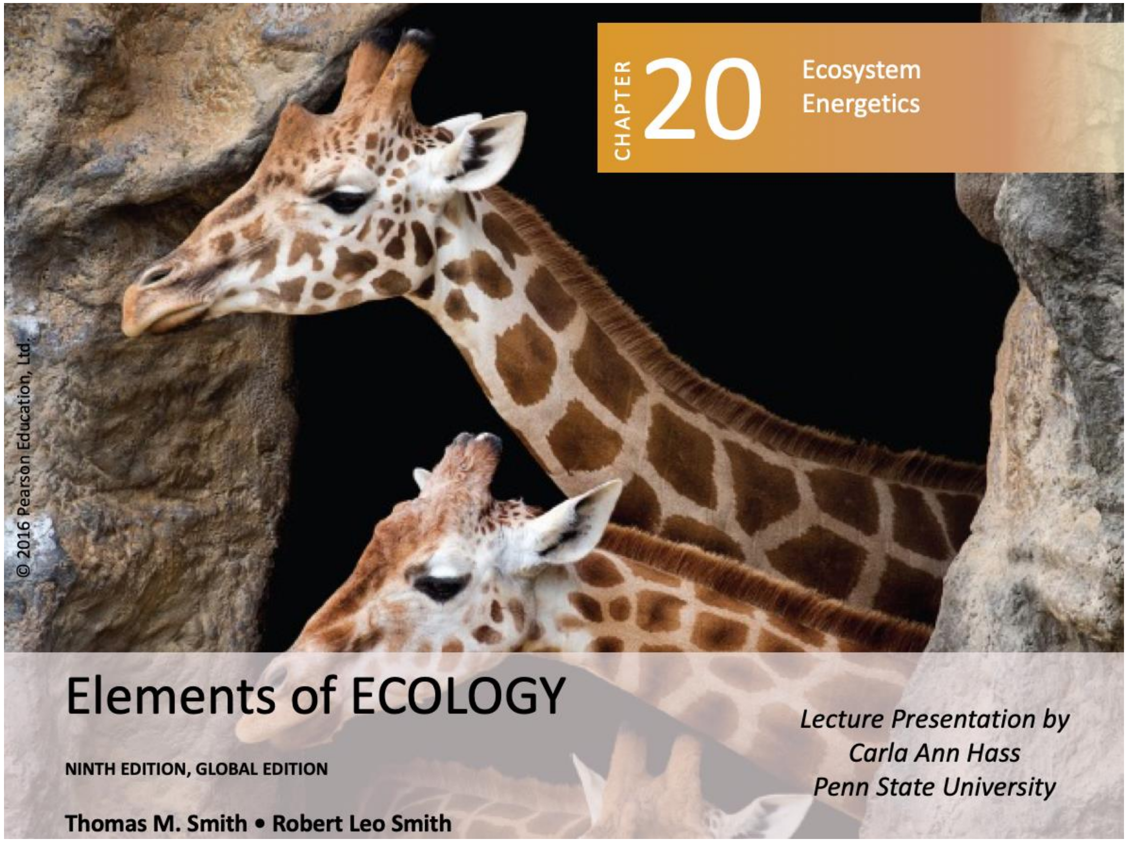
CHAPTER 20
Ecosystem Energetics
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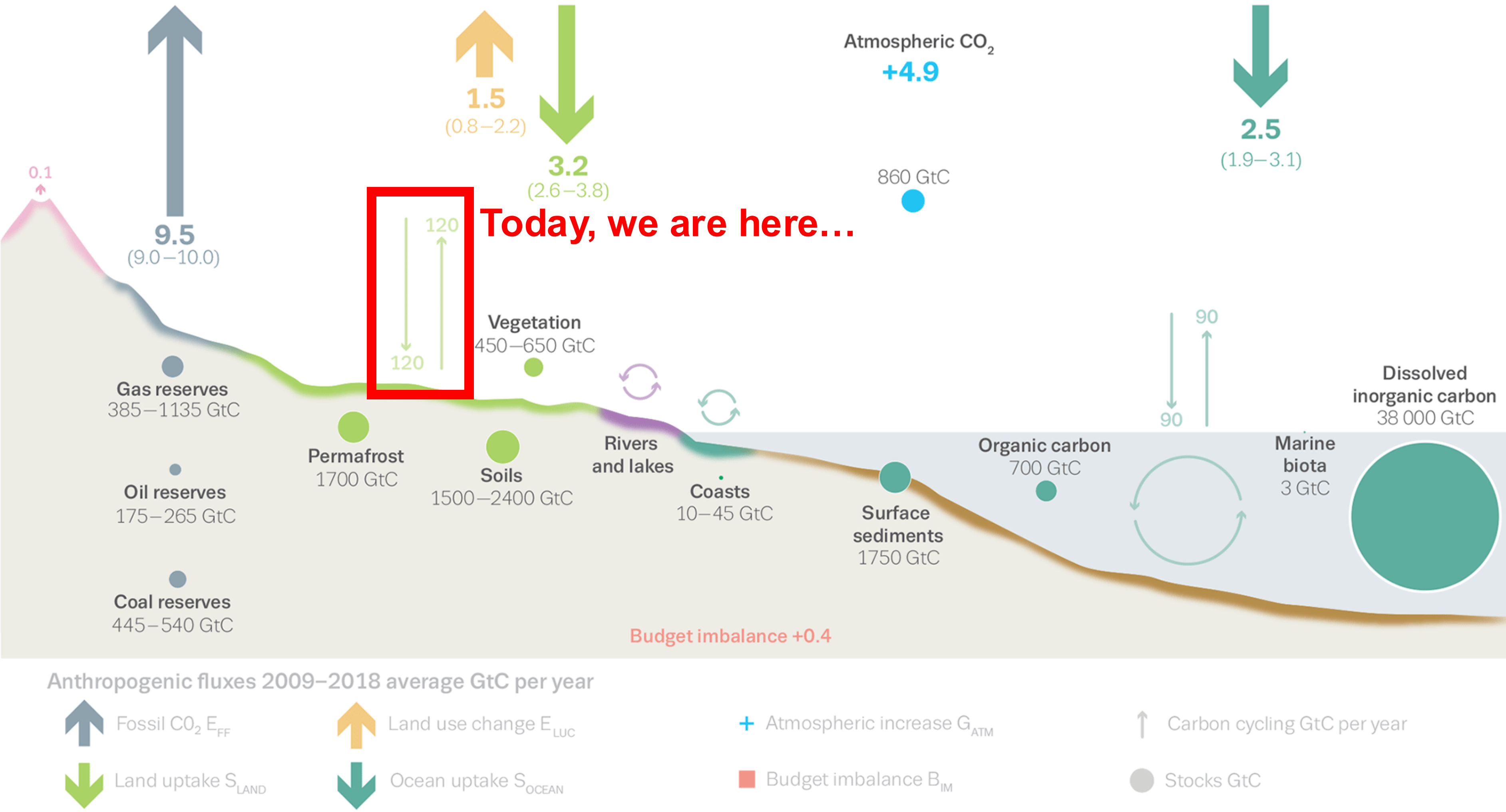
Elements of ECOLOGY
NINTH EDITION, GLOBAL EDITION
Thomas M. Smith • Robert Leo Smith
Lecture Presentation by
Carla Ann Hass
Penn State University

The global carbon cycle



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The sun is the major source of energy to life on Earth

Photons may be transformed into heat when they reach the atmosphere, land, or water. This heat energy warms the air, the surface of the land, the oceans, drives the water cycle, causes the wind and water currents.

Photons are also absorbed by photosynthetic organisms, which transform light energy into chemical bond energy, stored in carbon-based compounds ('sugars').

This energy can be transferred to higher trophic levels.

Energy and its transformations in ecosystems

- Energy can change from one form to another
- Energy can move from one place to another

Fluxes and transformation through a system independent of spatial and temporal scale

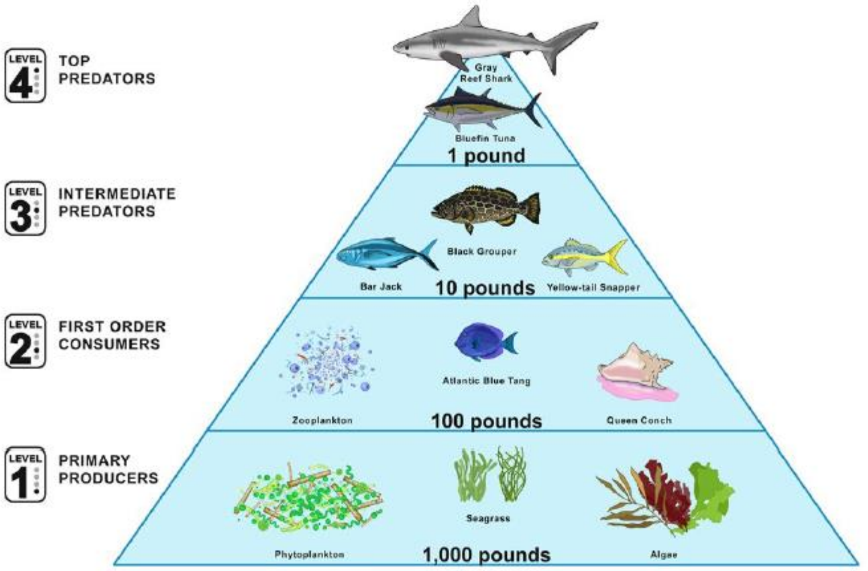
- Potential energy is stored energy; available for and capable of performing work
- Kinetic energy is the energy of motion, performing work
- Chemical energy is the energy of chemical substances that is released when the substances undergo a chemical reaction and transform into other substances (see catabolisms, anabolism)

In the reactions of photosynthesis, the reactants (simple molecules, such as CO_2) store less energy than the products (complex molecules, such as $C_6H_{12}O_6$). The extra energy stored in the products comes from solar radiation.

Primary Production

Secondary producers
(Consumers)

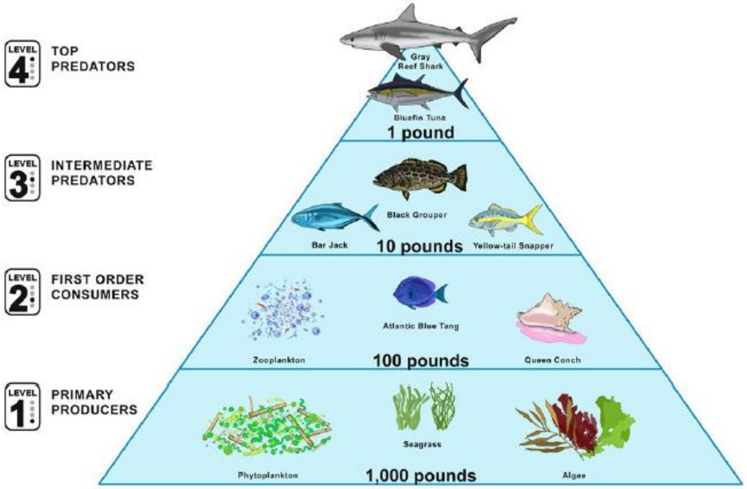
Primary producers
The vast majority of biomass on Earth



Energy fixed in the process of photosynthesis is primary production

Primary production is the rate at which autotrophs convert carbon dioxide (in the atmosphere or water) into organic compounds.

- Chemoautotrophs do this with energy from chemical compounds (oxidation of molecules that donate electrons).
- Photoautotrophs do this with energy from sunlight (photosynthesis).



Secondary production is the net energy allocated to the production of consumers.

It is the formation of living heterotrophic biomass over a period of time (grams per unit area per unit time). Secondary production is greatest when the birthrate of the population and the growth rate of individuals are highest.

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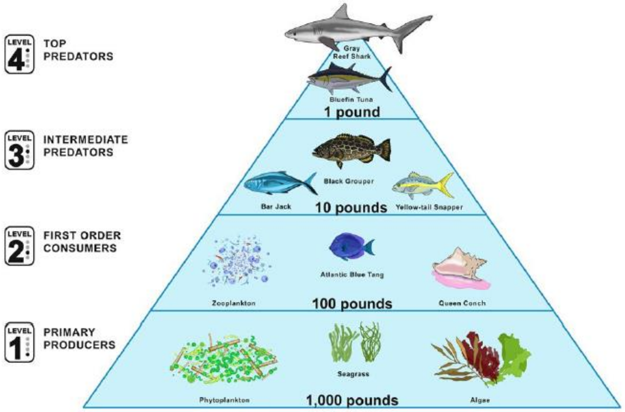
Energy fixed through photosynthesis is primary production

Gross primary production (GPP) is the total rate of photosynthesis (energy assimilated) by autotrophs.

Net primary production (NPP) is the rate of energy storage as organic molecules after energy is expended for cellular respiration (R): NPP = GPP – R.

GPP, NPP and R are ecosystem metabolic fluxes, of carbon grams carbon per square meter per year ($g/m^2/yr$).

Biomass (B) is the amount of accumulated organic matter found in an area at a given time; it can be expressed as grams of organic carbon per square meter (g/m^2); it is not the same as productivity because it is not a rate.



Terrestrial NPP can be measured by estimating the change in biomass over a given interval of time ($t_2 - t_1$): $\Delta B = B(t_2) - B(t_1)$.

There are two ways that biomass can be lost over the time period (D = death of plants, C = consumption of plants). Therefore, to estimate primary production from B: NPP = (ΔB) + D + C.

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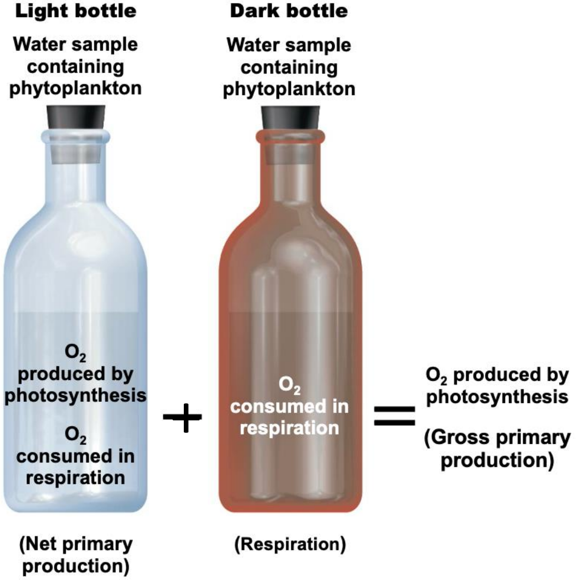
Energy fixed in the process of photosynthesis is primary production

In aquatic ecosystems, the classical method of estimating NPP is the light/dark bottle method where oxygen production/consumption can be measured.

Light bottles: The water sample containing phytoplankton (photoautotrophs) is incubated for a period of time. If photosynthesis exceeds respiration, then dissolved oxygen will accumulate (estimates NPP).

Dark bottles: Same sample incubated for same time period. If no photosynthesis, then only respiration, and dissolved oxygen will decline (estimates R).

The difference between the oxygen values in the two types of bottles estimates the total photosynthesis (GPP)



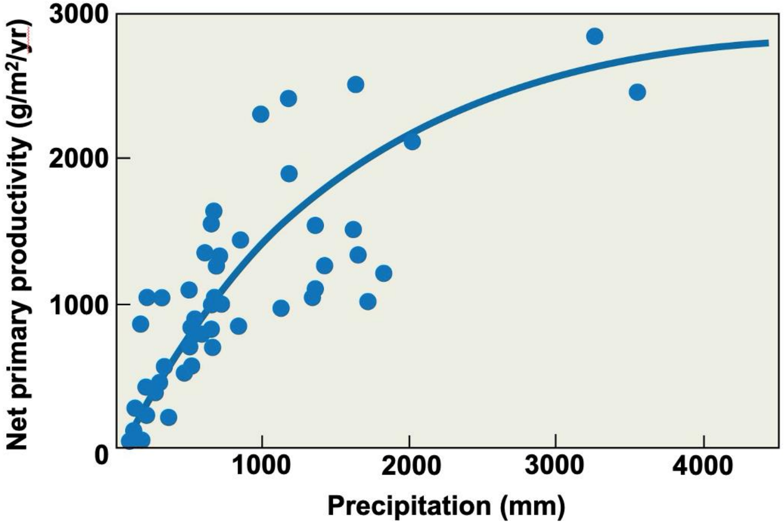
Paired light and dark bottles are used to measure photosynthesis (gross production), respiration, and net primary production by phytoplankton in aquatic ecosystems. A sample of water containing phytoplankton (primary producers) is placed in both bottles and allowed to incubate for a period of time. In the light (clear) bottle, O_2 is produced in photosynthesis and consumed in respiration. The resulting change (increase) in O_2 concentration represents the difference in the rates at which these two processes occur: net primary productivity. Lacking light to drive the process of photosynthesis, only respiration occurs in the dark bottle. As a result, O_2 concentration declines. The difference between the O_2 concentrations of the water from the light and dark bottles at the end of the incubation period represents the rate of O_2 produced in photosynthesis: gross primary productivity.

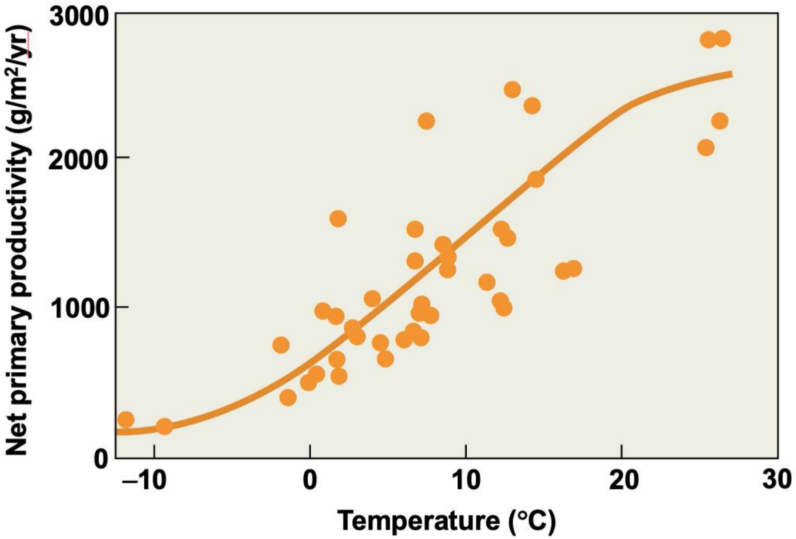
Climate and nutrient availability are the primary controls on net primary production in terrestrial ecosystems (see first class)

Many environmental factors, including climate, influence primary production in terrestrial ecosystems.

Terrestrial NPP increases with mean annual precipitation

Terrestrial NPP also increases with mean annual temperature. This increase is directly related to annual solar radiation.

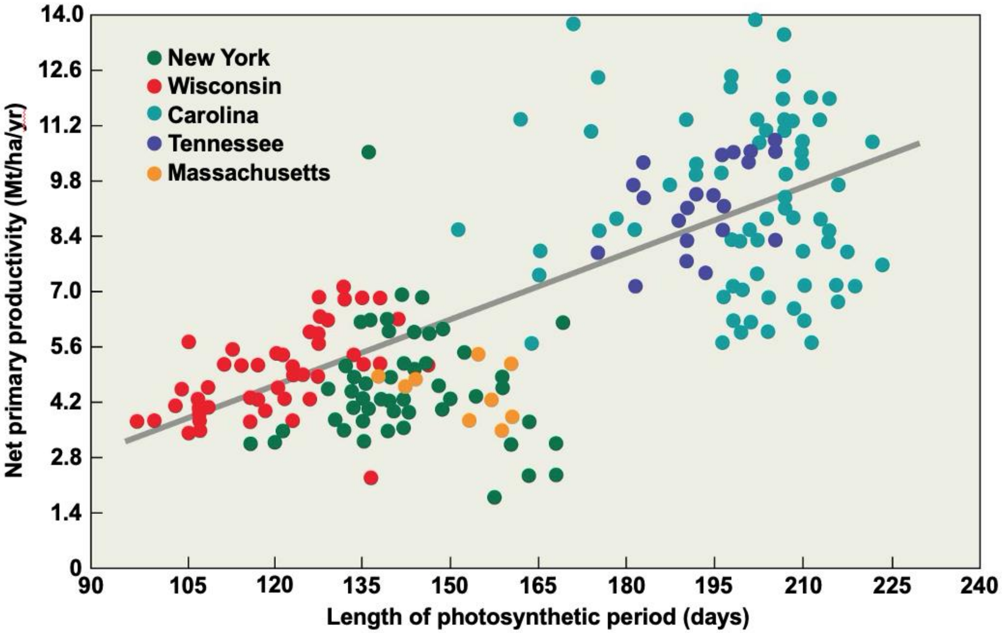




Net primary productivity for a variety of terrestrial ecosystems (a) as a function of mean annual precipitation and (b) as a function of mean annual temperature.

Climate and nutrient availability are the primary controls on net primary production in terrestrial ecosystems

Areas with higher mean daily temperatures also have <u>longer growing seasons, that is </u>the number of days with temperatures warm enough to support photosynthesis.



Relationship between net primary productivity and the length of the growing season for deciduous forest stands in eastern North America. Each point represents a single forest site. The (regression) line represents the general trend of increasing productivity with increasing length of the growing season (largely a function of latitude).

How does the interaction between mean annual precipitation and mean annual temperature affect NPP?

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Climate and nutrient availability are the primary controls on net primary production in terrestrial ecosystems

Photosynthesis requires CO_2 and water. Stomata open to take in CO_2, while water is lost through transpiration. This water is replaced through the roots, therefore more precipitation means more water is available for transpiration.

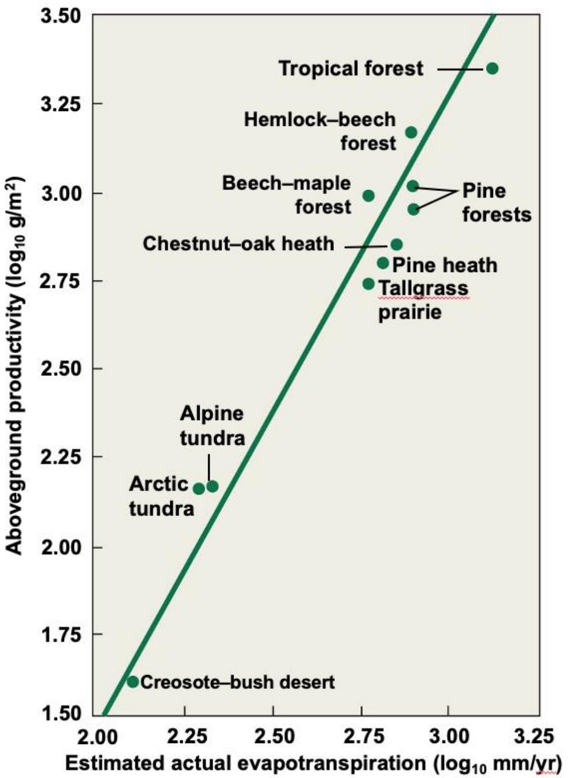
The amount of water available limits the rate of photosynthesis and hence primary productivity. The interaction of temperature and water availability affects NPP.

Warm air temperature increases transpiration rate required for cooling, and therefore the plant water demand. If water availability is low, NPP will be low.
Cool air temperature: NPP will be low, regardless of water availability.

At a similar mean annual temperature, low rainfall sites will have lower NPP, and high rainfall sites will have higher NPP.

Warm temperatures and adequate water supply give highest NPP.

See tropical versus boreal biomes!



Relationship between aboveground net primary productivity and (actual) evapotranspiration for a range of terrestrial ecosystems. Evapotranspiration—the combination of evaporation and transpiration at a site—depends on both precipitation and temperature

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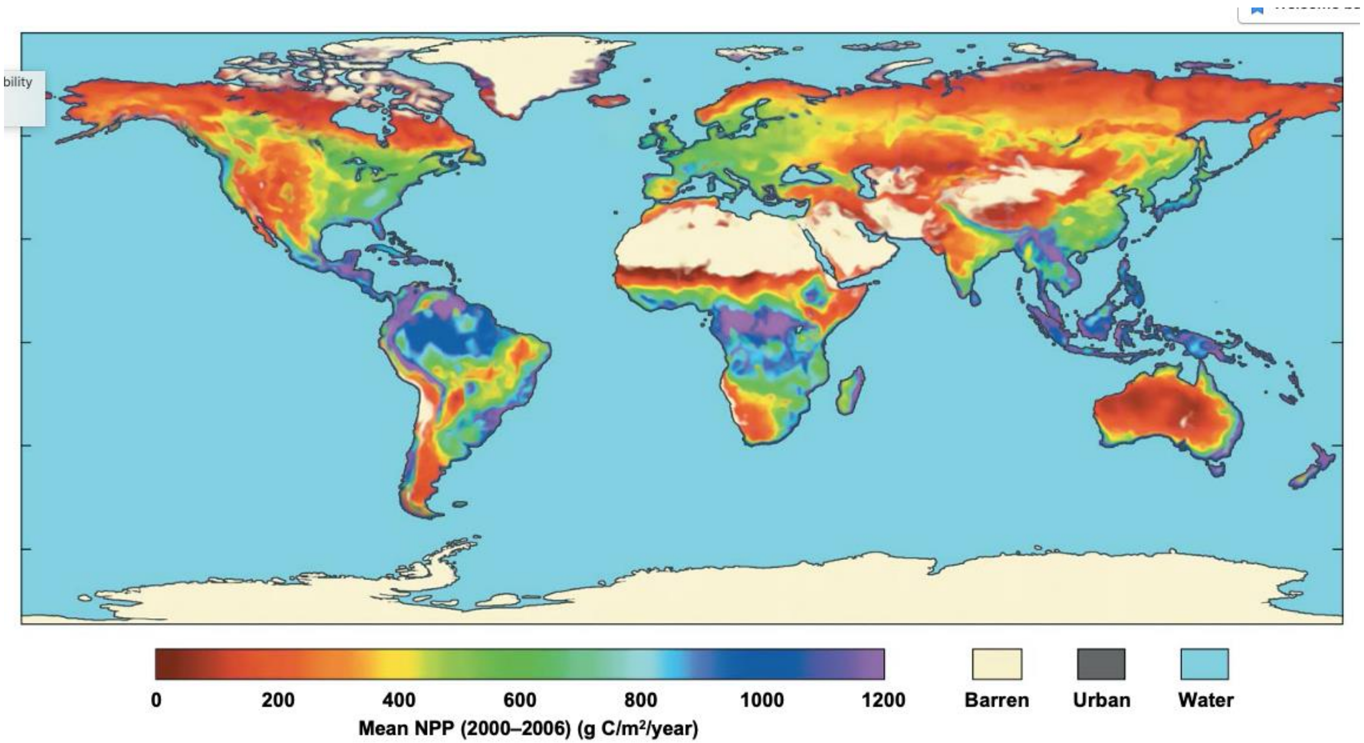
Climate and nutrient availability are the primary controls on net primary production in terrestrial ecosystems

Global patterns reflect the influence of temperature and precipitation on NPP



A global map of net primary productivity for the terrestrial ecosystems

Energy allocation and plant life-form influence primary production

Plant growth is a positive feedback system. If the rate of photosynthesis is held constant, the greater the allocation of carbon by the plant to photosynthetic tissues (leaves) versus non-photosynthetic tissues (stems and roots), and the greater the net carbon gain and plant growth.

NPP decreases as precipitation decreases. This is partially due to changing carbon allocation. Reduced soil moisture leads to increased allocation of carbon to roots instead of leaves by the plant, thereby reducing leaf area and net carbon gain (through photosynthesis).

Root-to-shoot ratio (R:S):

- 0.2 in tropical rain forest
- 4.5 in desert ecosystems

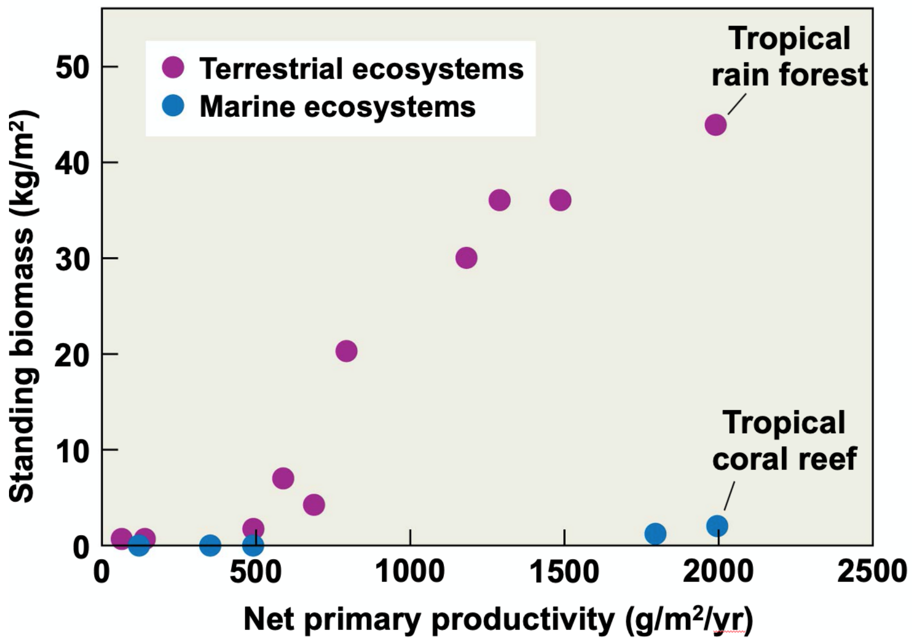
Carbon can also be allocated to structural defense mechanisms – protecting photosynthetic tissues, particulalrly in regions with poor precipitation.

Energy allocation and plant life-form influence primary production

The relative growth rate of primary producers differ between terrestrial and aquatic ecosystems.

The biomass gain per unit of plant biomass — equivalent to the relative net primary production (RNPP) – differs between the two ecosystems.

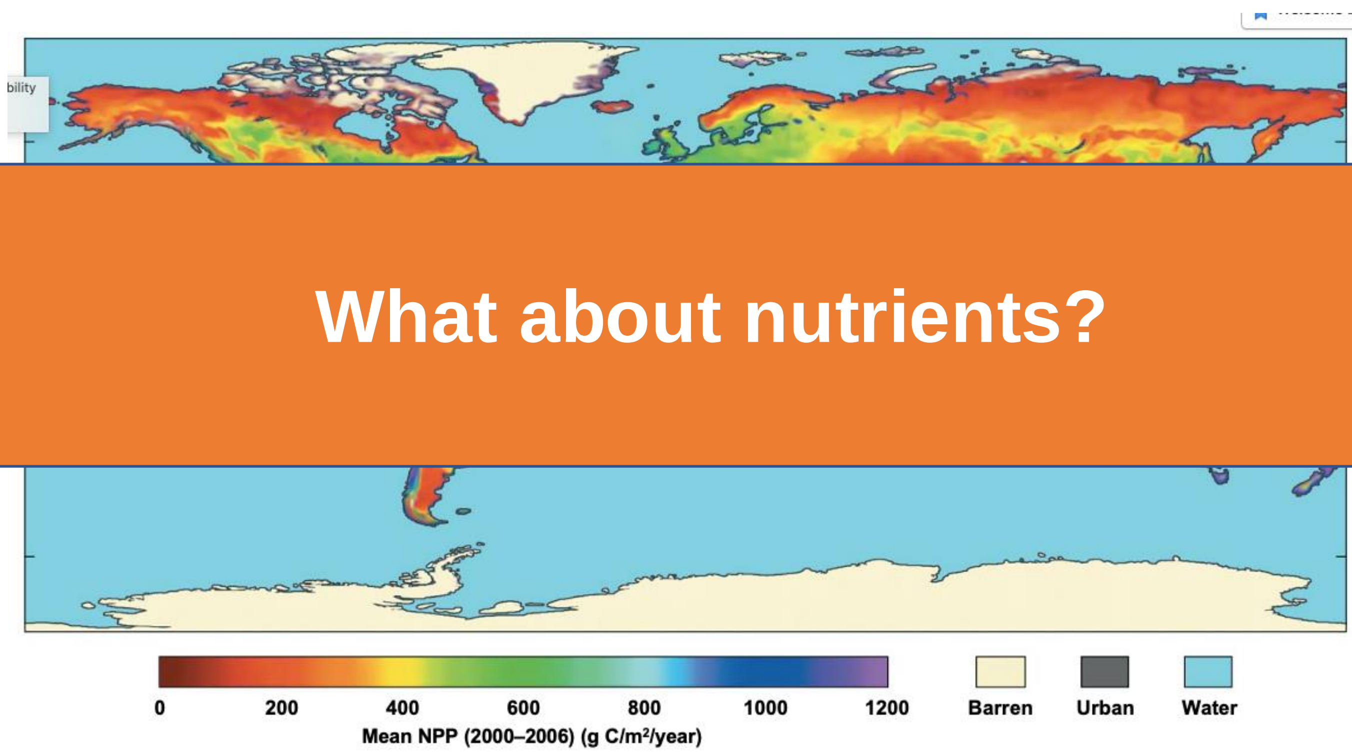
- Temperate forest: NPP = 1200 g/m²/yr, RNPP = 0.04 g/g/yr
- Temperate grassland: NPP = 550 g/m²/yr, RNPP = 0.031 g/g/yr
- Open ocean: RNPP = 42.3 g/g/yr



Higher biomass turnover in aquatic ecosystems; less structural elements required for aquatic primary producers because of the boyancy of water (uplift) and no rooting system (for phytoplankton)

Climate and nutrient availability are the primary controls on net primary production in terrestrial ecosystems

Global patterns reflect the influence of climate on NPP



What about nutrients?

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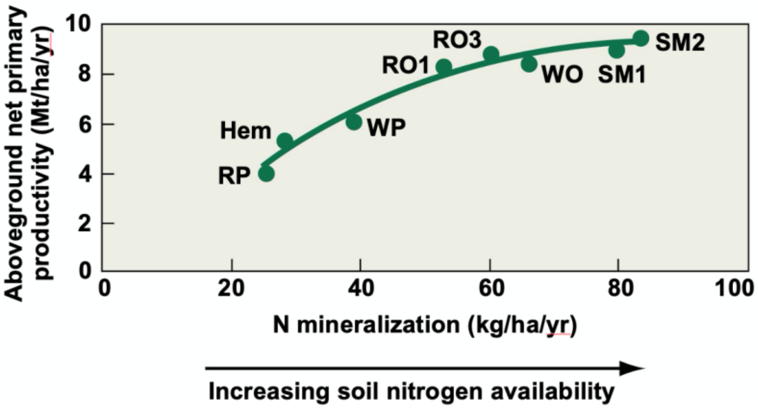
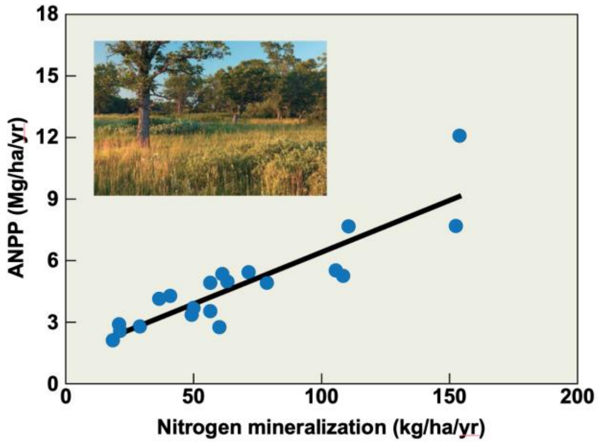
Climate and nutrient availability are the primary controls on net primary production in terrestrial ecosystems

- The availability of essential plant nutrients (e.g., N, P) affects ecosystem production.
- It influences the rate of nutrient uptake, photosynthesis, and plant growth.
- The general pattern is that NPP increases with increasing soil nutrient availability.



Relationship between net primary production and nutrient availability. Aboveground productivity increases with increasing nitrogen availability (N mineralization rate) for a variety of forest ecosystems on Blackhawk Island, Wisconsin. Abbreviations refer to the dominant trees in each stand: Hem, hemlock; RP, red pine; RO, red oak; WO, white oak; SM, sugar maple; WP, white pine.



Relationship between aboveground net primary productivity (ANPP) and nitrogen availability (nitrogen mineralization rate) for 20 oak savanna sites in Minnesota.

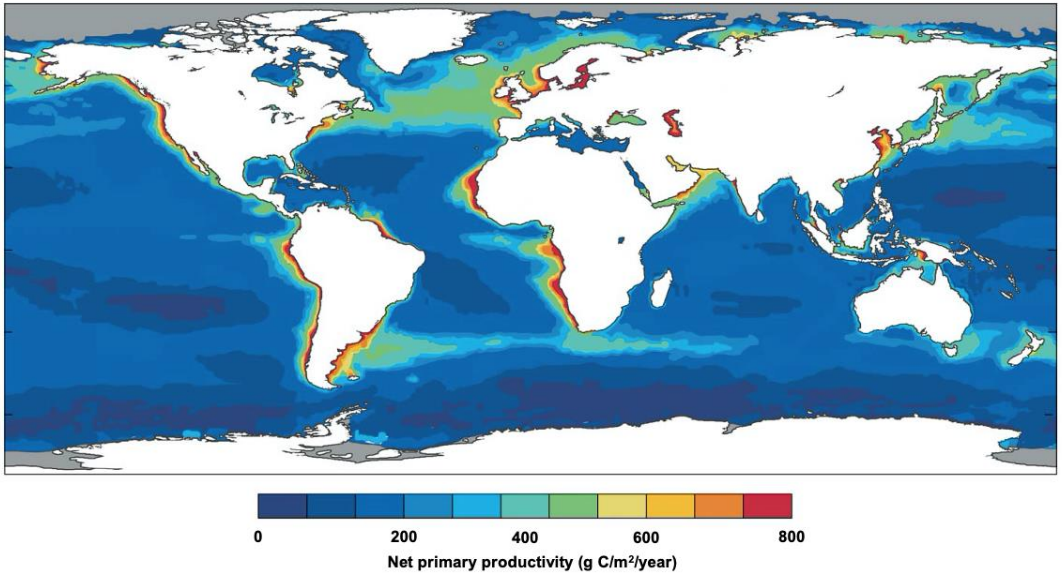
ANPP: Aboveground NPP

Light and nutrient availability are the primary controls on net primary production in aquatic ecosystems

Shallow waters in coastal environments of the oceans are the most productive marine ecosystems.

<u>Upwelling</u>: Shallow waters allow for a greater transport of nutrients from bottom sediments (remineralization) to the surface waters, assisted by wave action and tides.

Coastal waters receive nutrients from terrestrial ecosystems, transported by rivers.



Geographic variation in primary productivity of the world's oceans. Note that the highest productivity is along the coastal regions, and areas of lowest productivity are in the open ocean

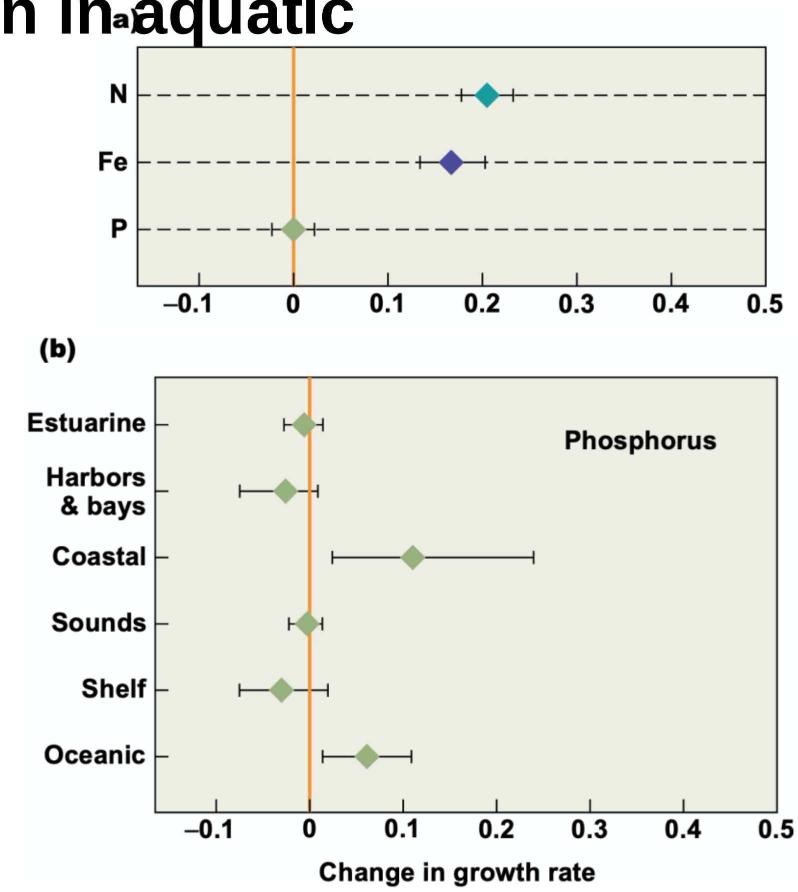
Light and nutrient availability are the primary controls on net primary production in aquatic ecosystems

Nutrient enrichment experiments have been conducted in the oceans worldwide.

Nitrogen addition stimulated phytoplankton growth the most. Iron followed closely in stimulating growth. These elements are limiting.

Phosphorus addition usually did not stimulate growth, except in the coastal and open ocean (less impacted by human activities/P deliveries).

These results are average responses and do not account for habitat differences.



(a) Effects of nutrient addition (nitrogen, iron, and phosphorus) on marine phytoplankton growth rates in 303 experiments. Changes in growth rate measured as change in per unit (per gram, per unit carbon, or per unit chlorophyll), a growth rate of an algal community following the addition of surplus nutrients. Diamonds represent mean values from the experiments, and the bars represent 95 percent confidence intervals. The solid orange line represents zero effect. Mean response values are based on 148 (N), 114 (P), and 35 (Fe) experiments. **(b)** The change in phytoplankton growth rate as a result of the phosphorus addition varied among different marine environments.

Light and nutrient availability are the primary controls on net primary production in aqua ecosystems

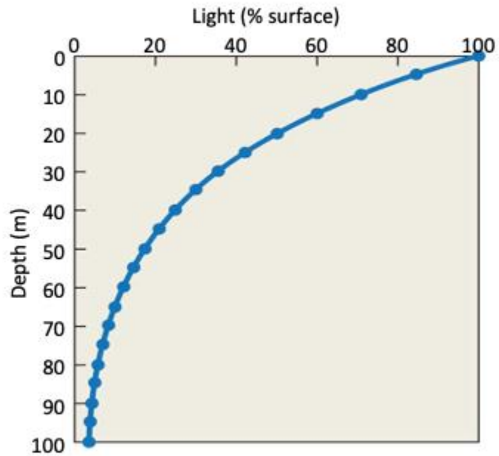
Photosynthetically active radiation (PAR) declines exponentially with water depth.

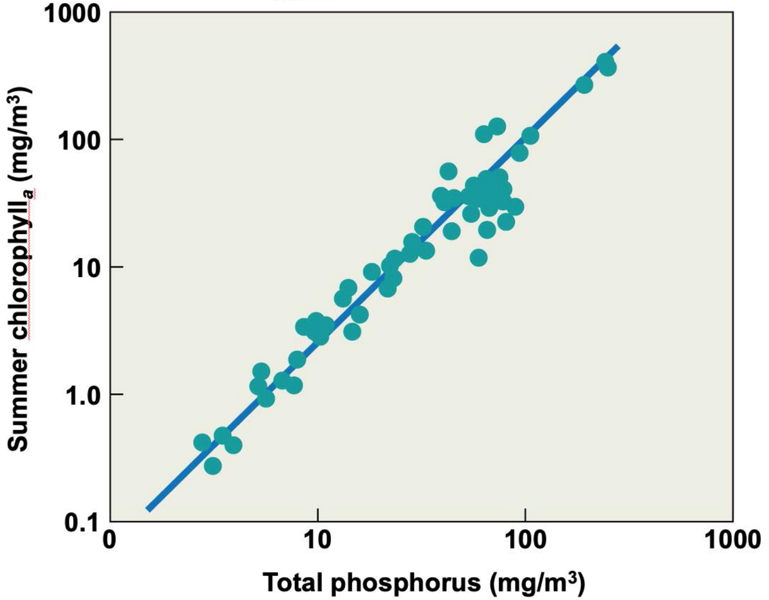
Photosynthetic rate and therefore GPP of phytoplankton are highest at intermediate levels of PAR (photoinhibition at higher PAR). Respiration rate is fairly constant as depth increases. For phytoplankton deeper in the water column, light intensity and photosynthesis decrease.

Where GPP = R, NPP = 0; this is the compensation depth, the transition from the productive to the decomposition zone in the water column.

Clear pattern of increasing NPP with increasing phosphorus concentration.

Phosphorus is often limiting. If available in excess, it can lead to lake eutrophication.





Relationship between summer average chlorophyll (an estimate of phytoplankton net primary productivity) content (*y*-axis) and spring total phosphorus concentration (*x*-axis) for northern temperate lake ecosystems (each point represents a single lake).

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Light and nutrient availability are the primary controls on net primary production in aquatic ecosystems

Lake eutrophication

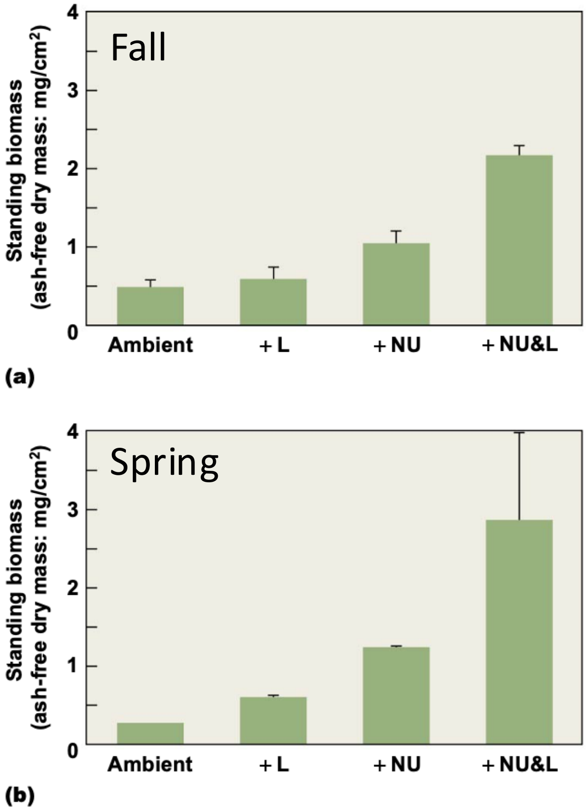
- Hypoxia (< 2 mg O_2 / L)
- Toxins from cyanobacterial blooms
- Biodiversity loss and fish killing

Light and nutrient availability are the primary controls on net primary production in aquatic ecosystems

NPP in stream ecosystems is limited by both light and nutrient availability.

Study in which light and nutrient concentrations were manipulated in experimental stream channels:

- Light availability limited production during summer. Greatest leaf canopy cover reduced light levels to the lowest values.
- Nutrients were more limiting during fall and spring when the canopy is more open and light levels increase.
- Greatest increases in biomass were seen when both light and nutrients were enhanced



Standing biomass (periphyton) in experimental stream channels under different treatments during the last week of (a) fall experiment (11/3 – 12/20) and (b) spring experiment (3/7 – 4/26). Ambient: shaded, low nutrient treatment; +L, high light, low nutrient treatment; +NU, shaded, high nutrient treatment; +NU&L, high light, high nutrient treatment.

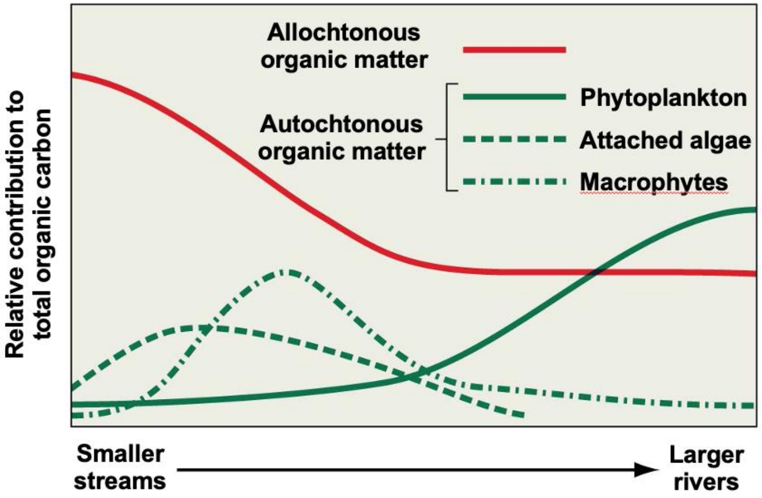
External inputs of organic carbon can be important to aquatic ecosystems

<u>Autochthonous organic carbon is produced within an ecosystem</u>. It comes from photosynthesis by aquatic photoautotrophs (plants, algae, phytoplankton).

<u>Allochthonous organic carbon is produced outside of an ecosystem</u>. It comes from dead organic matter input from adjacent terrestrial ecosystems can be dissolved (DOM) or particulate (POM) organic matter. Importance of allochthonous sources of carbon varies among different aquatic ecosystems

<u>Small streams in forests</u> – allochthonous carbon from surrounding forests predominate (from dead plant material). Shading by trees limits photoautotrophs in the stream.

<u>Marine ecosystems and large lakes</u>: autochthonous inputs predominate (from phytoplankton)



What happens as the stream widens farther downstream and transitions to a river? Trees live along the banks. Shading becomes limited to the margins of the stream. More light is available, and NPP by plants, algae, and phytoplankton increases. Autochthonous carbon becomes more important.

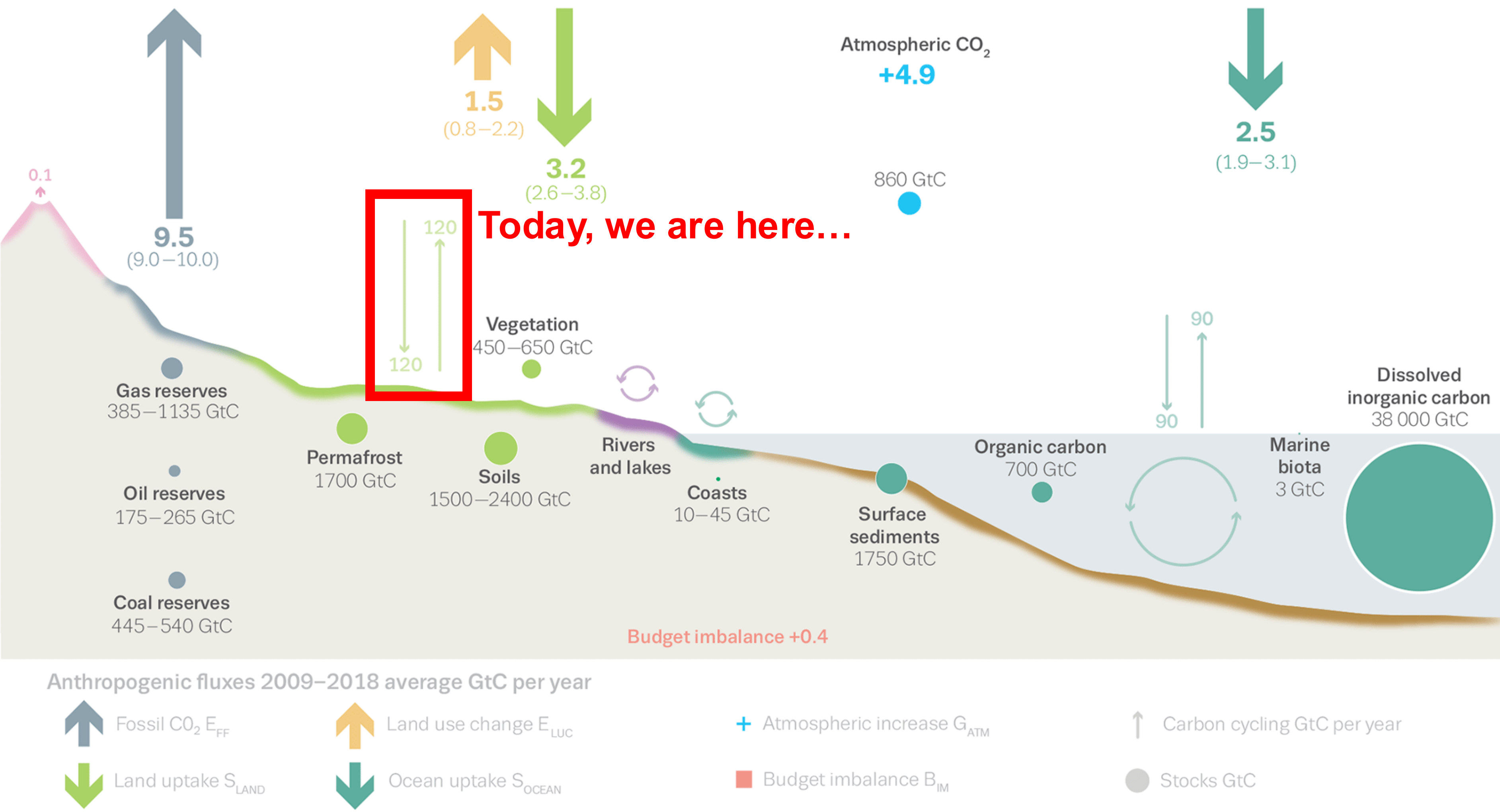
External Inputs of Organic Carbon Can Be Important to Aquatic Ecosystems

Large lakes: Autochthonous inputs of organic matter usually predominate; vary seasonally with the volume of water flowing into the lake.

Small lakes: Allochthonous inputs of organic matter can be significant. Up to 50 percent of the organic carbon in the food chain can be allochthonous.

From primary production to secondary production

The global carbon cycle



From primary production to secondary production

NPP is the energy that is in principle available to heterotrophic (satisfying their energy demand from organic carbon) in an ecosystem.

What is the fate of NPP in an ecosystem?
How can NPP move to other ecosystems?

Herbivores or detritivores eventually consume almost all primary productivity. What happens to this energy when consumed?

Some passes from the body as waste (feces and urine), some is assimilated and can be used for metabolism and heat, for maintenance acquiring food and performing work (e.g., muscle contractions, repairing the organism's body)

The remaining energy can be used for growth of new tissues and reproduction.

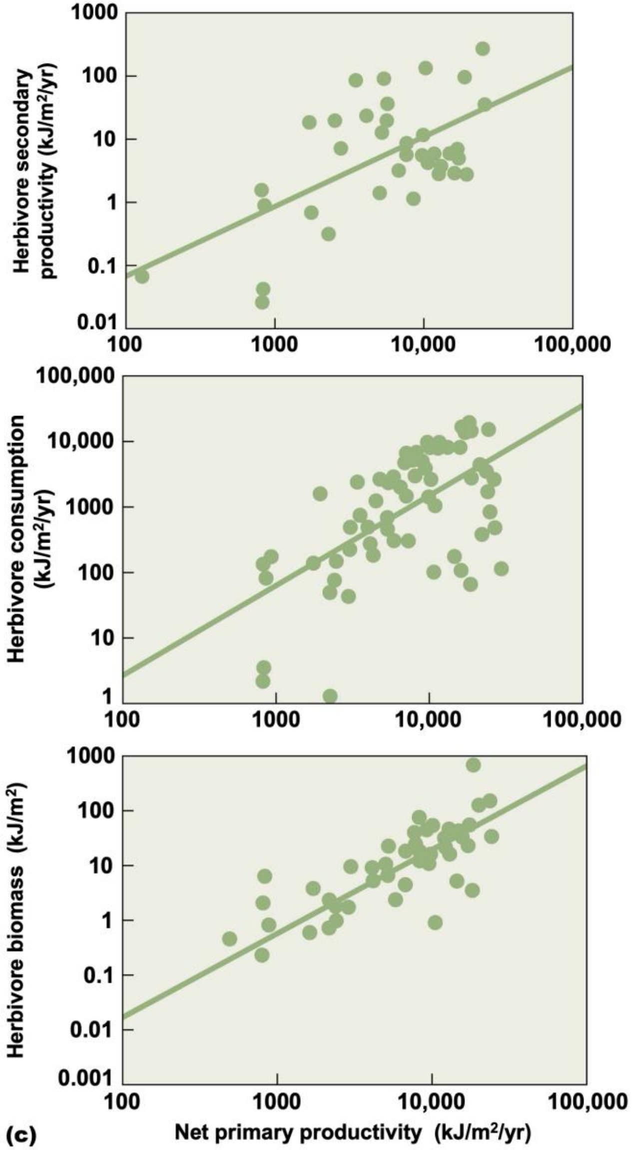
Primary production limits secondary production

Secondary production depends on primary production as its energy source.

Terrestrial ecosystems: Primary production functions as a constraint on secondary production – that is, a bottom-up control.

As primary production increases, herbivore biomass, consumption and secondary production increase. Energy from the 'green' basis is transported upwards through the food web.

Relationship between aboveground net primary productivity and (a) net secondary productivity of herbivores, (b) consumption, and (c) herbivore biomass. Units are KJ/m²/yr except for biomass, which is KJ/m². Each point represents a different terrestrial ecosystem.
(Adapted from McNaughton et al. 1989; Nature Publishing Group.)



Primary production limits secondary production

Secondary production depends on primary production for energy.

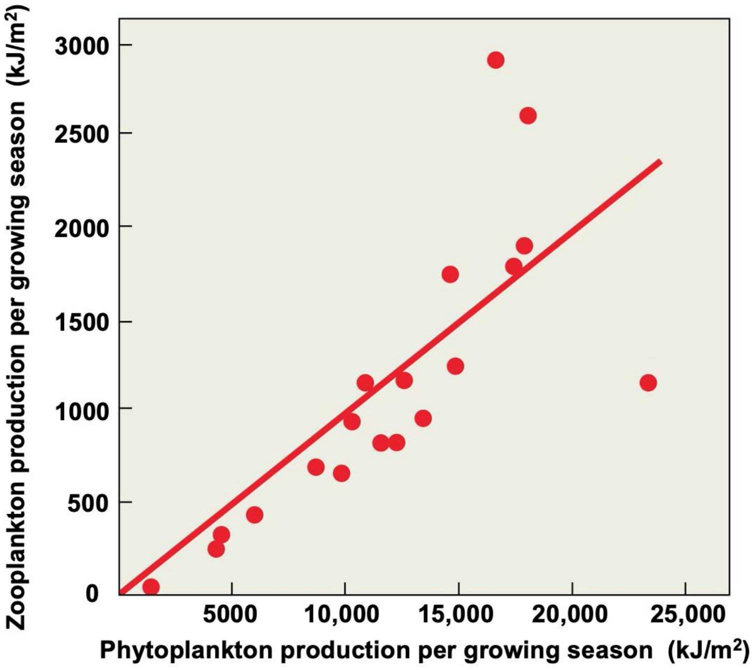
<u>Aquatic ecosystems</u>: A similar relationship is seen between phytoplankton (primary productivity) and zooplankton (secondary productivity) in lake ecosystems.

Significant positive relationship between phytoplankton productivity and productivity of herbivorous and carnivorous zooplankton.

These studies suggest <u>bottom-up control</u> of energy flow through the ecosystems.

The populations and productivity of autotrophs control the populations and productivity of heterotrophs.

Food webs present a more complex picture of interactions among autotroph, herbivore, and carnivore populations
What about top-down controls?



Relationship between phytoplankton (primary) and zooplankton (secondary) productivity in lake ecosystems. (Adapted from Brylinsky and Mann 1973.)

Primary production limits secondary production

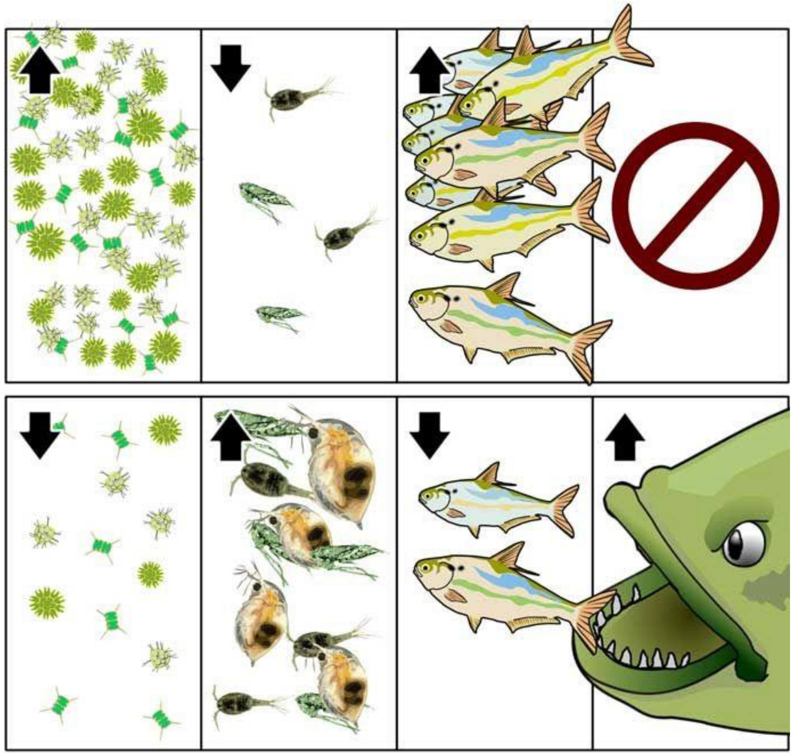
Top-down versus bottom-up

The world is ‘green’: Plant biomass accumulates because predators keep herbivore populations in check.

Experiments suggest that top-down controls are important in many ecosystems.

Patterns of NPP are influenced by abiotic conditions (e.g., light, nutrients) and predator controls on herbivore populations.

Top-down control results in a trophic cascade, important in controlling community structure and NPP in aquatic and terrestrial ecosystems.



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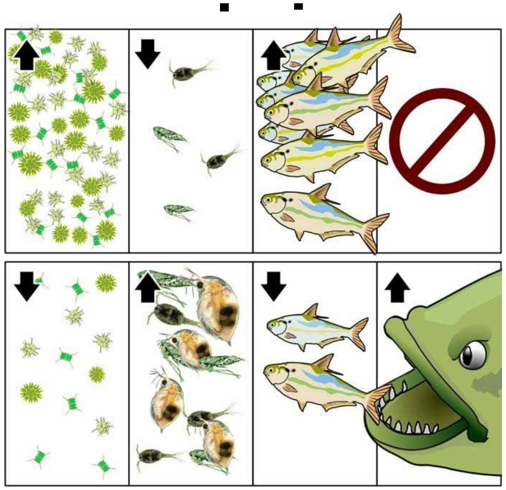
Trophic Transfer Efficiency and food



Ecosystems have two major food chains

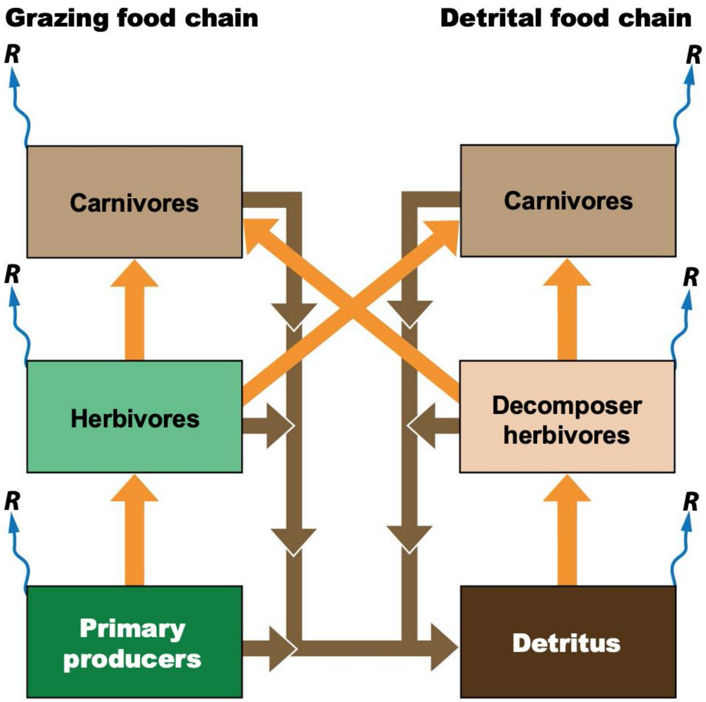
A food chain describes the series of steps by which the energy stored in autotrophs is passed through the ecosystem.

Within a food chain, all organisms that obtain their energy in the same number of steps from autotrophs (primary producers) are members of the same trophic level: first level (primary producers), second level (first-level consumers or herbivores), higher levels (second-level consumers or carnivores).

Major feeding groups are based on a common energy source: <u>autotrophs, herbivores, carnivores</u>. <u>Omnivores</u> occupy more than one trophic level. Each feeding group is linked to others in a way that represents energy flow.

There are two major food chains in any ecosystem:

<u>Grazing (green) food chain</u> – source of energy for the herbivores is living plant biomass (NPP).
<u>Detrital (brown) food chain</u> – source of energy for the decomposers is dead organic matter or detritus snails, millipedes, earthworms, fungi, bacteria.



Two parts of any ecosystem: a grazing food chain and a detrital food chain. Orange arrows linking trophic levels represent the flow of energy associated with ingestion. The blue arrows from each trophic level represent the loss of energy through respiration. The brown arrows represent a combination of dead organic matter (unconsumed biomass) and waste products (feces and urine).

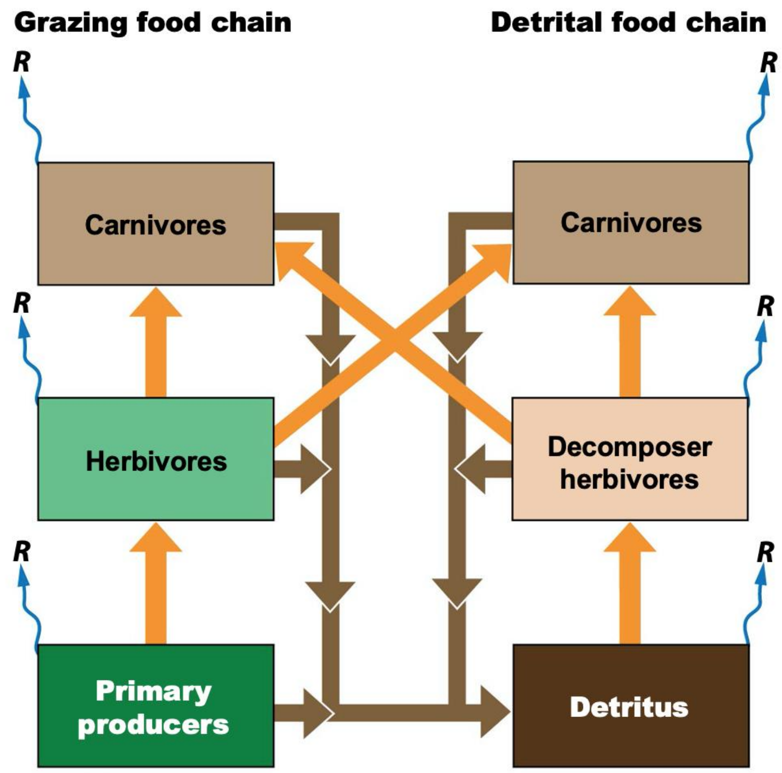
Ecosystems Have Two Major Food Chains

A food chain describes the series of steps by which the energy stored in autotrophs is passed through the ecosystem.

<u>These two food chains are linked</u>. The source of energy for the detrital food chain is the grazing food chain's dead organic material and waste.

Energy flow is unidirectional in the grazing food chain; it is not unidirectional in the detrital food chain. Dead organic material and waste from each level return as inputs to the base of the food chain.

At higher levels, carnivores from both food chains feed on herbivores from both food chains.



Two parts of any ecosystem: a grazing food chain and a detrital food chain. Orange arrows linking trophic levels represent the flow of energy associated with ingestion. The blue arrows from each trophic level represent the loss of energy through respiration. The brown arrows represent a combination of dead organic matter (unconsumed biomass) and waste products (feces and urine).

Consumers vary in efficiency of production

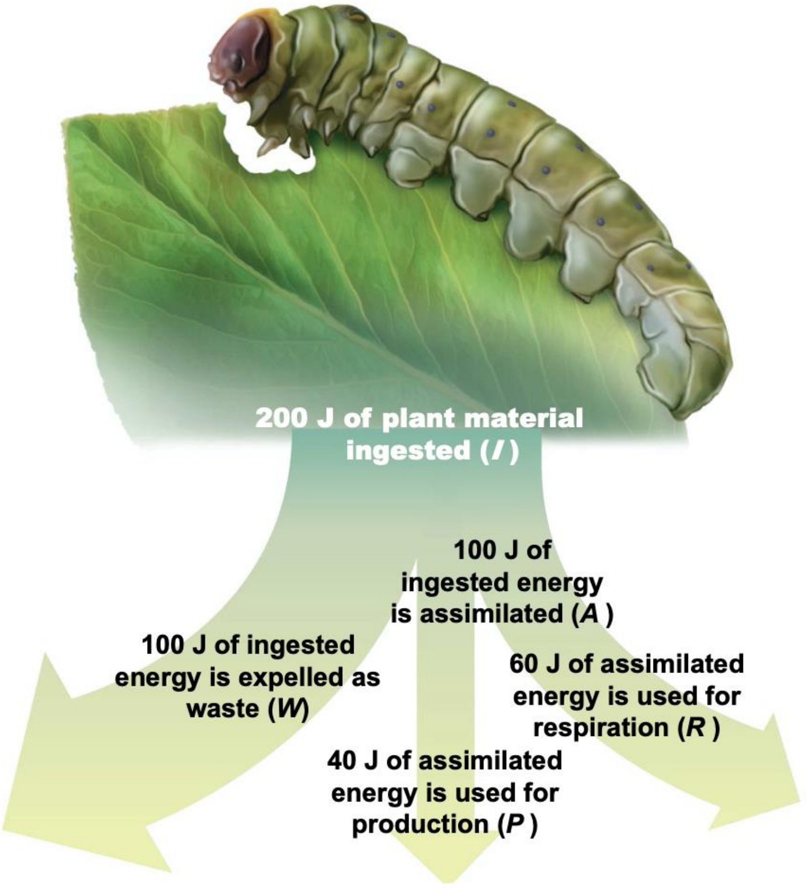
There is variation among consumers in their efficiency of converting energy consumed into secondary production

The food ingested by a consumer (I) can be assimilated in the gut (A) or expelled from the body as waste (W).

The energy that is assimilated (A) can be used in respiration (R) or used for production (P).

<u>Assimilation efficiency</u> (A/I) measures the efficiency of extracting energy from food.

<u>Production efficiency</u> (P/A) measures how efficiently assimilated energy is incorporated into secondary production



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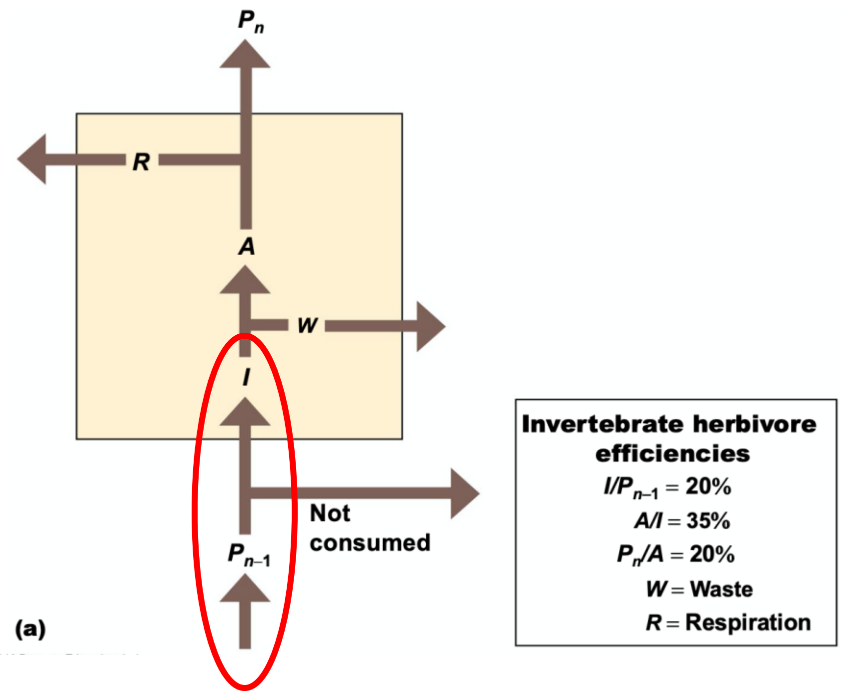
Energy flows through trophic levels can be quantified

The energy available to a given trophic level (n) is the net production of the next-lower level (n - 1).

The energy available for grazing herbivores (level 2) is net primary production (level 1).

Some part of this productivity is consumed or ingested (I). Of this, some is assimilated (A) and the rest is lost as waste (W). Of the energy assimilated, some is lost to respiration (R), the rest goes to production (P), which is then available to the next level.

This flow is quantified as the assimilation efficiency (A/I) and production efficiency (P/A), and consumption efficiency, which is the ratio of ingestion to production at the next-lower trophic level: I_n/P_{n-1}.



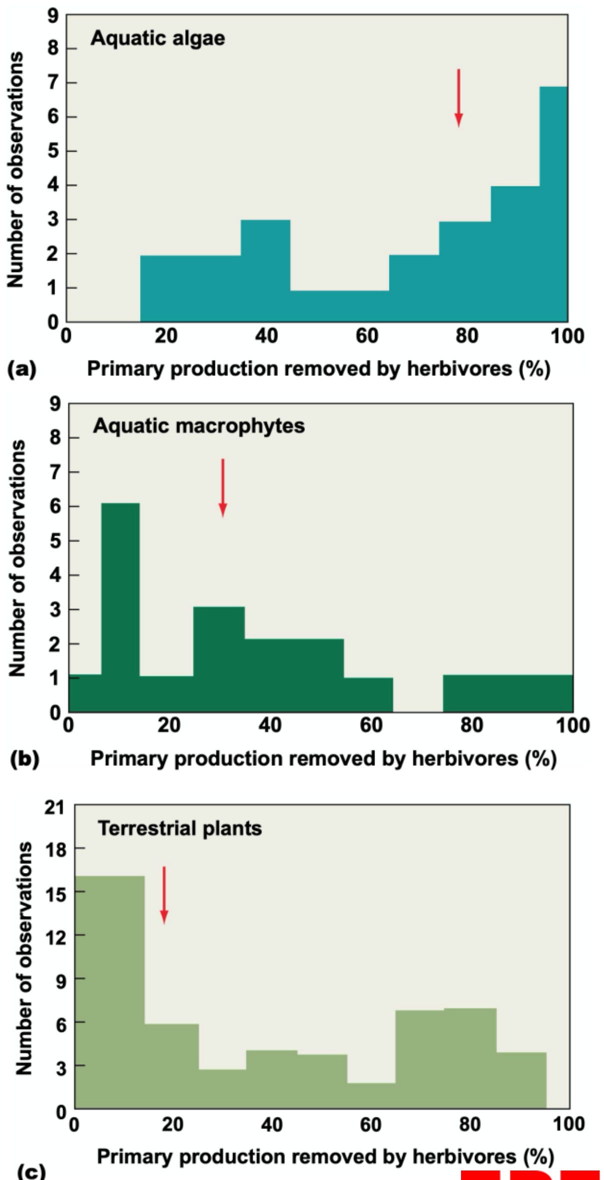
Energy flow within a single trophic compartment. (b) An example of quantifying energy flow for an invertebrate herbivore using estimates of efficiencies provided in table. Values are in kilocalories (kcal).

Consumption efficiency determines the pathway of energy flow through the ecosystem

The relative importance of the grazing and detrital food chains, and the rate of energy flow through the trophic levels can vary widely among different types of ecosystems

Values of consumption efficiency determine the pathway of energy flow through a food chain and allow comparisons of energy flow through different ecosystems.

Grazing herbivores play the dominant role in energy flow in some open-water aquatic ecosystems when dominated by aquatic algae (phytoplankton) – median of 79 percent.



Results from a review of studies that examined rates of herbivory in different ecosystems. Histograms represent the percentage of net primary productivity consumed by herbivores in ecosystems dominated by (a) algae (phytoplankton), (b) rooted aquatic plants, and (c) terrestrial plants. Number of observations refers to the number of experiments having a given level of consumption. Red arrows indicate the median value. Note that herbivores consume a significantly greater proportion of phytoplankton productivity than do either aquatic or terrestrial plants. (Adapted from Cyr and Pace 1993.)

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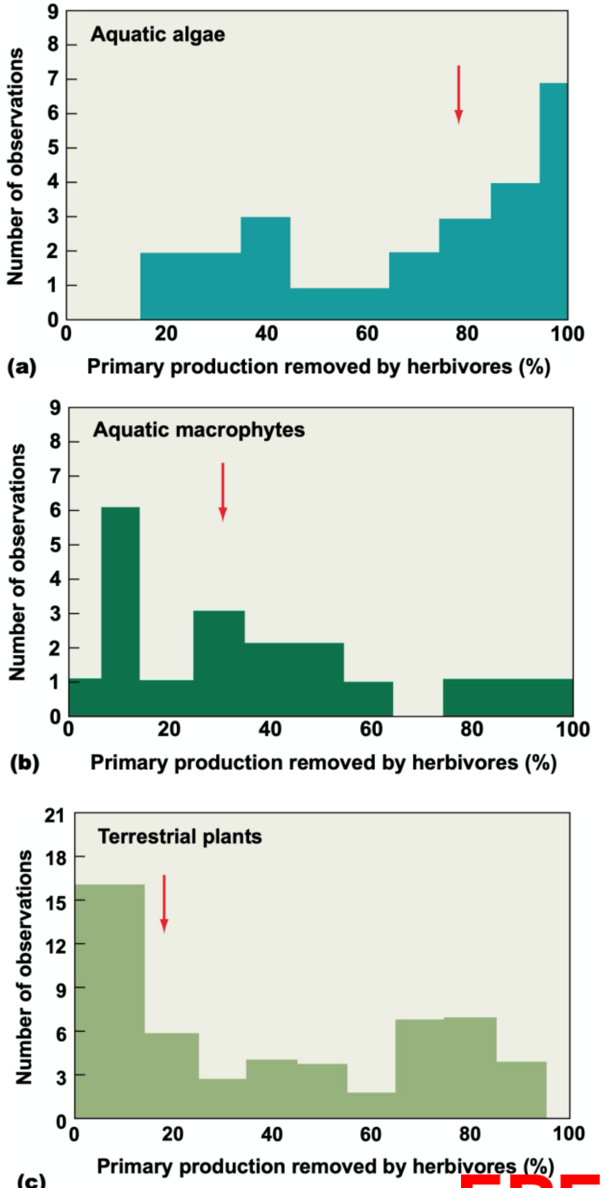
Consumption efficiency determines the pathway of energy flow through the ecosystem

Aquatic ecosystems in which algae (phytoplankton) dominate have high rates of herbivory; aquatic ecosystems with macrophytes have a lower rate of herbivory – median value of 30 percent – and the detrital food chain is dominant.

In terrestrial ecosystems, only 17 percent of primary production of the vascular plants is removed by herbivores, so the detrital food chain is also dominant.

<u>What may explain this gradient in herbivory consumption efficiency?</u>

Results from a review of studies that examined rates of herbivory in different ecosystems. Histograms represent the percentage of net primary productivity consumed by herbivores in ecosystems dominated by (a) algae (phytoplankton), (b) rooted aquatic plants, and (c) terrestrial plants. Number of observations refers to the number of experiments having a given level of consumption. Red arrows indicate the median value. Note that herbivores consume a significantly greater proportion of phytoplankton productivity than do either aquatic or terrestrial plants. (Adapted from Cyr and Pace 1993.)



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Energy decreases in each successive trophic level

The quantity of energy flowing into a trophic level decreases with each successive trophic level in the food chain

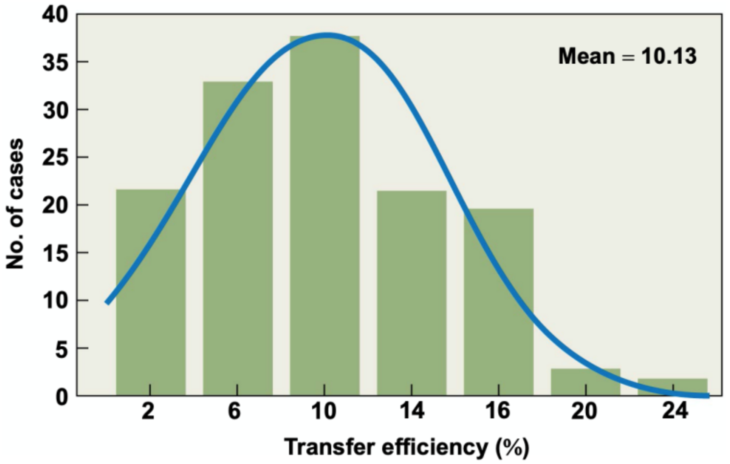
Trophic efficiency (TE) measures the transfer of energy between trophic levels.

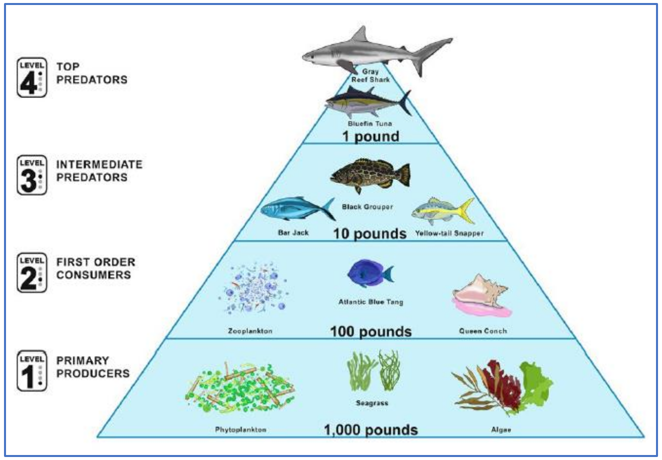
It is the ratio of the productivity in a given trophic level (P_n) to the trophic level its organisms feed on (P_{n-1})

$$TE = P_n/P_{n-1}$$

An important consequence of this decreasing energy transfer from one trophic level to the next is the decrease in biomass of organisms within each successive level.

Therefore, the biomass in each trophic level can be shown as a pyramid.

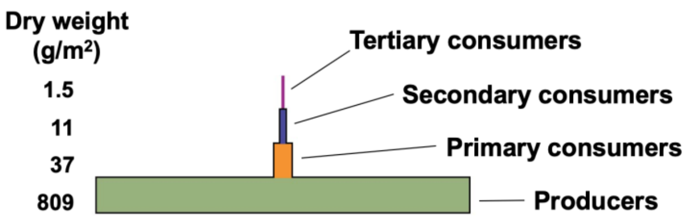




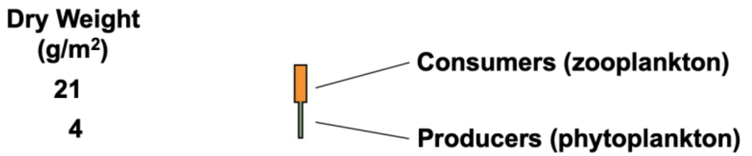
Energy decreases in each successive trophic level

In general, the biomass of producers must be greater than that of the herbivores. The biomass of herbivores must be greater than that of the carnivores.

In aquatic ecosystems, the biomass of small, short-lived phytoplankton is much less than that of the larger, herbivorous, longer-lived zooplankton



(a) Florida bog



(b) English Channel

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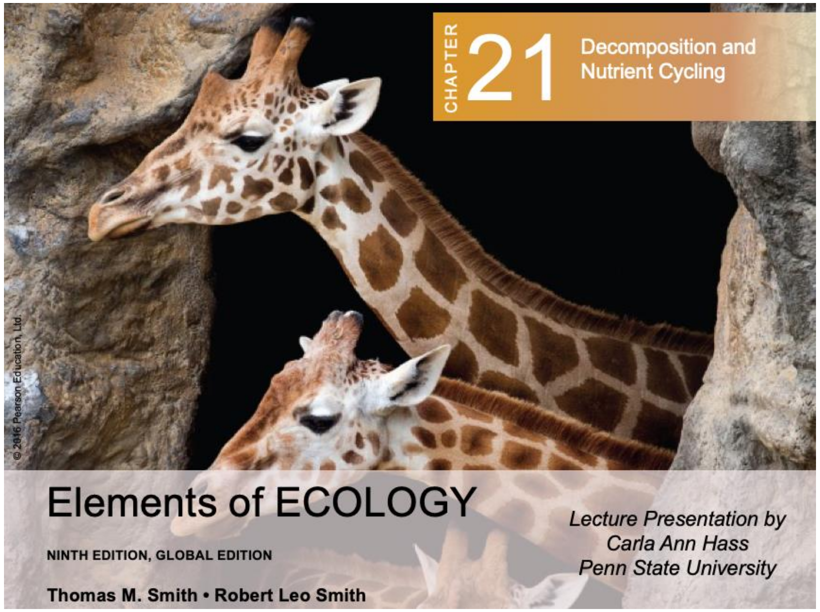
Key words

- Primary production and controls (water, light, nutrients)
- Secondary production relies on primary production
- Food chains and trophic transfer
- Energy flow through food chains

Next week:

Decomposition and nutrient cycling



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