

Work of Sousa

Wayne Sousa (1979), who studied the effects of disturbance on the diversity of sessile marine algae and invertebrates growing on intertidal boulders, found support for the intermediate disturbance hypothesis. Diversity in prairie vegetation also appears to be higher in areas receiving intermediate levels of disturbance. The effect of disturbance on diversity appears to depend upon a trade-off between dispersal and competitive abilities.

Human disturbance

Human disturbance is an ancient feature of the biosphere. Human influences touch every portion of the biosphere and have done so for thousands of years. For instance, humans disturbed tropical rain forests in Central America beginning about 11,000 years ago.

Intermediate disturbance hypothesis

The effects of human disturbance fall within the framework of the intermediate disturbance hypothesis. Though intense human disturbance reduces species diversity, moderate levels of disturbance may increase the diversity of some communities such as the European chalk grasslands.

65 Food Webs

A food web summarizes the feeding relations in a community. The earliest work on food webs concentrated on simplified communities in areas such as the Arctic islands. However, researchers such as Charles Elton (1927) soon found that even these so-called simple communities included very complex feeding relations. The level of food web complexity increased substantially, however, as researchers began to study complex communities. Studies of the food webs of tropical freshwater fish communities revealed highly complex networks of trophic interaction that persisted even in the face of various simplifications. A focus on strong interactions can simplify food web structure and identify those interactions responsible for most of the energy flow in communities.

Food web and structure of communities

The feeding activities of a few keystone species may control the structure of communities. Robert Paine (1966) proposed that the feeding activities of a few species have inordinate influences on community structure. He predicted that some predators may increase species diversity by reducing the probability of competitive exclusion. Manipulative studies of predaceous species have identified many keystone species, including starfish and snails in the marine intertidal zone and fish in rivers. On land, birds exert substantial influences on communities of their arthropod prey.

Jane Lubchenko (1978)

Jane Lubchenko (1978) demonstrated that the influence of consumers on community structure depends upon their feeding preferences, their local population density, and the relative competitive abilities of prey species. Keystone species are those that, despite low biomass, exert strong effects on the structure of the communities they inhabit.

Exotic predators and the structure of food webs

Exotic predators can collapse and simplify the structure of food webs. Introduced fishes have devastated the native fishes of Lake Atitlan and Gatun Lake in Central America.

Examples

The influence of the Nile perch on the fish community of Lake Victoria is enmeshed with massive changes in the lake's ecosystem. Introduction of the Nile perch is rapidly reducing the species-rich fish fauna of Lake Victoria to a community dominated by a handful of species.

Humans

Humans have acted as keystone species in communities. People have long manipulated food webs both as a consequence of their own feeding activities and by introducing or deleting species from existing food webs. In addition, many of these manipulations have been focused on keystone species. Hunters in tropical rain forests have been responsible for removing keystone animal species from large areas of the rain forests of Central and South America. Chinese farmers have used ants as keystone predators to control pests in citrus orchards for over 1,700 years.

66 Primary Production and Energy Flow

Flow of energy

We can view a forest, a stream, or an ocean as a system that absorbs, transforms, and stores energy. In this view, physical, chemical, and biological structures and processes are inseparable. When we look at natural

systems in this way we view them as ecosystems. An ecosystem is a biological community plus all of the abiotic factors influencing that community.

Production

- **Primary production**, the fixation of energy by autotrophs, is one of the most important ecosystem processes.
- The **rate of primary production** is the amount of energy fixed over some interval of time.
- **Gross primary production** is the total amount of energy fixed by all the autotrophs in the ecosystem. Net primary production is the amount of energy left over after autotrophs have met their own energetic needs.

Terrestrial primary production

Terrestrial primary production is generally limited by temperature and moisture. The variables most highly correlated with variation in terrestrial primary production are temperature and moisture. Highest rates of terrestrial primary production occur under warm, moist conditions.

Annual Actual Evapo Transpiration (AET)

Temperature and moisture conditions can be combined in a single measure called annual actual evapotranspiration, or AET, which is the total amount of water that evaporates and transpires off a landscape during the course of a year. Annual AET is positively correlated with net primary production in terrestrial ecosystems. However, significant variation in terrestrial primary production results from differences in soil fertility.

Aquatic primary production

Aquatic primary production is generally limited by nutrient availability. One of the best documented patterns in the biosphere is the positive relationship between nutrient availability and rate of primary production in aquatic ecosystems.

Phosphorus concentration usually limits rates of primary production in freshwater ecosystems, while nitrogen concentration usually limits rates of marine primary production.

Exmaples

- Consumers can influence rates of primary production in aquatic and terrestrial ecosystems. Piscivorous fish can indirectly reduce rates of primary production in lakes by reducing the density of plankton-feeding fish..
- Reduced density of planktivorous fish can lead to increased density of herbivorous zooplankton, which can reduce the densities of phytoplankton and rates of primary production. Intense grazing by large mammalian herbivores on the Serengeti increases annual net primary production by inducing compensatory growth in grasses

Energy losses

Energy losses limit the number of trophic levels in ecosystems. Ecosystem ecologists have simplified the trophic structure of ecosystems by arranging species into trophic levels based upon the predominant source of their nutrition. A trophic level is determined by the number of transfers of energy from primary producers to that level.

Energy losses and trophic levels

As energy is transferred from one trophic level to another, energy is lost due to limited assimilation, respiration by consumers, and heat production. As a result of these losses, the quantity of energy in an ecosystem decreases with each successive trophic level, forming a pyramid-shaped distribution of energy among trophic levels. As losses between trophic levels accumulate, eventually there is insufficient energy to support a viable population at a higher trophic level.

Stable isotope analysis

Stable isotope analysis can be used to trace the flow of energy through ecosystems. The ratios of different stable isotopes of important elements such as nitrogen and carbon are generally different in different parts of ecosystems.

Use of Stable isotope analysis

As a consequence, ecologists can use isotopic ratios to study the trophic structure and energy flow through ecosystems. **Stable isotope analysis** has helped **quantify dietary composition of wild populations** and the major sources of energy used by prehistoric human populations.

67 Nutrient Cycling and Retention

Nutrient cycling

The elements organisms require for development, maintenance, and reproduction are called nutrients. Ecologists refer to the use, transformation, movement, and reuse of nutrients in ecosystems as nutrient cycling.

Nutrient cycling is one of the most ecologically significant processes studied by ecosystem ecologists. The carbon, nitrogen, and phosphorus cycles have played especially prominent roles in studies of nutrient cycling.

Decomposition rate

Decomposition rate is influenced by temperature, moisture, and chemical composition of litter and the environment. The rate of decomposition affects the rate at which nutrients, such as nitrogen and phosphorus, are made available to primary producers. Rates of decomposition in terrestrial ecosystems are higher under warm, moist conditions. The rate of decomposition in terrestrial ecosystems increases with nitrogen content and decreases with the lignin content of litter. The chemical composition of litter and the availability of nutrients in the surrounding environment also influence rates of decomposition in aquatic ecosystems.

Cycling of nutrients in ecosystems

- Plants and animals can modify the distribution and cycling of nutrients in ecosystems.
- The dynamics of nutrients in streams are best represented by a spiral rather than a cycle.
- The length of stream required for an atom of a nutrient to complete a cycle is called the spiraling length.
- Stream macroinvertebrates can substantially reduce spiraling length of nutrients in stream ecosystems.
- Animals can also alter the distribution and rate of nutrient cycling in terrestrial ecosystems. Nitrogen-fixing plants increase the quantity and rates of nitrogen cycling in terrestrial ecosystems.

Disturbance and nutrient loss from ecosystems

Disturbance increases nutrient loss from ecosystems. Vegetation exerts substantial control on nutrient retention by terrestrial ecosystems. Vegetative controls on nutrient loss from forest ecosystems appear to be most important in environments that are warm and moist during the growing season

Nutrient enrichment by humans

Vegetative controls appear to be less important in cold and/or dry environments. Nutrient loss by stream ecosystems is highly pulsed and associated with disturbance by flooding. Nutrient enrichment by humans is altering aquatic and terrestrial ecosystems. Nitrate concentration and export by the earth's major rivers correlate directly with human population density. Human disturbance also increases export of phosphorus from aquatic catchments. Nutrient enrichment appears to be reducing the diversity of plants and fungi in terrestrial ecosystems. Land managers around the world use nutrient loading models to predict and manage the impact of land use on aquatic ecosystems.

68 Succession and Stability

Primary succession

Succession is the gradual change in plant and animal communities in an area following disturbance

or the creation of new substrate. Primary succession occurs on newly exposed geological substrates not significantly modified by organisms.

Secondary succession

Secondary succession occurs in areas where disturbance destroys a community without destroying the soil. Succession generally ends with a climax community whose populations remain stable until disrupted by disturbance.

Community changes during succession

Community changes during succession include increases in species diversity and changes in species composition. Primary forest succession around Glacier Bay may require about 1,500 years, while secondary forest succession on the Piedmont Plateau takes about 150 years.

Succession duration

Meanwhile, succession in the intertidal zone requires 1 to 3 years and succession within a desert stream occurs in less than 2 months. Despite the great differences in the time required, all these Successional sequences show increased species diversity over time.

Ecosystem changes during succession

Ecosystem changes during succession include increases in biomass, primary production, respiration, and nutrient retention. Succession at Glacier Bay produces changes in several ecosystem properties, including increased soil depth, organic content, moisture, and nitrogen. Over the same successional sequence, several soil properties show decreases, including soil bulk density, pH, and phosphorus concentration. Succession at the Hubbard Brook Experimental Forest increased nutrient retention by the forest ecosystem.

Predictability of succession

Several ecosystem properties change predictably during succession in Sycamore Creek, Arizona, including biomass, primary production, respiration, and nitrogen retention.

Mechanisms of succession

Mechanisms that drive ecological succession include facilitation, tolerance, and inhibition.

Most studies of succession support the facilitation model, the inhibition model, or some combination of the two.

Both facilitation and inhibition occur during intertidal succession. Facilitation and inhibition also occur during secondary and primary forest succession.

Community stability

Community stability may be due to lack of disturbance or community resistance or resilience in the face of disturbance. Ecologists generally define stability as the persistence of a community or ecosystem in the face of disturbance. Resistance is the ability of a community or ecosystem to maintain structure and/or function in the face of potential disturbance.

Resilience

The ability to bounce back after disturbance is called resilience. A resilient community or ecosystem may be completely disrupted by disturbance but quickly return to its former state. Studies of the Park Grass Experiment suggest that our perception of stability is affected by the scale of measurement. Studies in Sycamore Creek indicate that resilience is sometimes influenced by resource availability and that resistance may result from landscape-level phenomena

Repeat photography

Repeat photography can be used to detect long-term ecological change. Most successional sequences and most community and ecosystem responses to climatic change take place over very long periods of time. Repeat photography has become a valuable tool to help ecologists study these long-term changes.

69 Landscape Ecology

Landscape:

A landscape is a heterogeneous area composed of several ecosystems. The ecosystems making up a landscape generally form a mosaic of visually distinctive patches. These patches are called landscape elements. Landscape ecology is the study of landscape structure and processes.

Landscape structure

Landscape structure includes the size, shape, composition, number, and position of different ecosystems within a landscape. Most questions in landscape ecology require that ecologists quantify landscape structure. Until recently, however, geometry, which means “earth measurement,” could offer only rough approximations of complex landscape structure.

Structure of complex natural shapes

Today, an area of mathematics called fractal geometry can be used to quantify the structure of complex natural shapes. One of the findings of fractal geometry is that the length of the perimeter of complex shapes depends upon the size of the device used to measure the perimeter. One implication of this result is that organisms of different sizes may use the environment in very different ways

Landscape structure influences Ecological processes

Landscape structure influences processes such as the flow of energy, materials, and species between the ecosystems within a landscape. Landscape ecologists have proposed that landscape structure, especially the size, number, and isolation of habitat patches, can influence the movement of organisms between potentially suitable habitats. The group of subpopulations living on such habitat patches make up a metapopulation.

Examples

- Studies of the movements of small mammals in a prairie landscape show that a smaller proportion of individuals moves in more fragmented landscape but that the individuals that do move will move farther. The local population density of the Glanville fritillary butterfly, *Melitaea cinxia*, is lower on larger and on isolated habitat patches. Small populations of this butterfly and desert bighorn sheep are more vulnerable to local extinction.
- The source of water for lakes in a Wisconsin lake district is determined by their positions in the landscape, which in turn determine their hydrologic and chemical responses to drought.

Landscapes are structured and dynamic

Landscapes are structured and change in response to geological processes, climate, activities of organisms, and fire.

Geological features produced by processes such as volcanism, sedimentation, and erosion interact with climate to provide a primary source of landscape structure. In the Sonoran Desert, plant distributions map clearly onto soils of different ages and form a vegetative mosaic that closely matches soil mosaics. This mosaic will gradually shift as geological processes and climate gradually change the soil mosaic. While geological processes and climate set the basic template for landscape structure, the activities of organisms, from plants to elephants, can be an additional source of landscape structure and change.

Human activity changes the structure of landscapes

Economically motivated human activity changes the structure of landscapes all over the globe. Beavers can quickly change landscape structure and processes over large regions. Fire contributes to the structure of landscapes ranging from tropical savanna to boreal forest. However, fire plays a particularly prominent role in regions with a Mediterranean climate. Because human activity has often altered landscape structure and processes in undesirable ways, there is growing pressure and interest in landscape restoration. Some of the most ambitious current restoration efforts focus on the restoration of riverine landscapes. Rivers and their floodplains form a complex, highly dynamic landscape that includes river riparian forest, marsh, oxbow lake, and wet meadow' ecosystems.

Water management and landscapes

Over the past century, water management by building dams, channelizing rivers, constructing flood levees, and diverting water for irrigation has cut the historic connections between most rivers and their floodplains. The restoration of the Kissimmee River landscape is also one of the largest ecological experiments ever conducted and will be a significant test of the predictive ability of ecological theory.

70 Geographic Ecology

Geographic ecology focuses on large-scale patterns of distribution and diversity of organisms, such as island biogeography, latitudinal patterns of species diversity, and the influences of large-scale regional and historical processes on biological diversity.

Isolation

On islands and habitat patches on continents, species richness increases with area and decreases

with isolation. Larger oceanic islands support more species of most groups of organisms than small islands. Isolated oceanic islands generally contain fewer species than islands near mainland areas. Many habitats on continents are so isolated that they can be considered as islands.

Species richness on habitat islands

Species richness on habitat islands, such as mountain islands in the American Southwest, increases with area and decreases with isolation. Lakes can also be considered as habitat islands. They are aquatic environments isolated from other aquatic environments by land. Fish species richness generally increases with lake area. Species richness is usually negatively correlated with island isolation. However, because organisms differ substantially in dispersal rates, an island that is very isolated for one group of organisms may be completely accessible to another group.

Models of Species richness on islands

Species richness on islands can be modelled as a dynamic balance between immigration and extinction of species.

The equilibrium model of island biogeography proposes that the difference between rates of immigration and extinction determines the species richness on islands.

The equilibrium model of island biogeography

The equilibrium model of island biogeography assumes that rates of species immigration to islands are mainly determined by distance from sources of immigrants. The model assumes that rates of extinction on islands are determined mainly by island size.

Species richness and latitude

Species richness generally increases from middle and high latitudes to the equator. Most groups of organisms are more species-rich in the tropics.

Many factors may contribute to higher tropical species richness, including

- (1) time since perturbation,
- (2) productivity,
- (3) environmental heterogeneity,
- (4) favorableness,
- (5) niche breadths and interspecific interactions, and
- (6) differences in speciation and extinction rates. Several lines of evidence support the hypothesis that differences in surface area play a primary role in determining latitudinal gradients in species richness

Structure of biotas and ecosystems

Long-term historical and regional processes significantly influence the structure of biotas and ecosystems. Much geographic variation in species richness can be explained by historical and regional processes.

Exceptional situations

Some exceptional situations that seem to have resulted from unique historical and regional processes include the exceptional species richness of the Cape floristic region of South Africa, the high species richness of temperate trees in east Asia, and the low bird diversity in beech forests of South America.

A word of advise

The ecologist interested in understanding large-scale patterns of species richness must consider processes occurring over similarly large scales and over long periods of time.

Global positioning systems

Global positioning systems, remote sensing, and geographic information systems are important tools for effective geographic ecology. A global positioning system determines locations on the earth's surface, including latitude, longitude, and altitude, using satellites as reference points.

Remote sensing satellites

Remote sensing satellites are generally fitted with electro-optical sensors that scan several bands of the electromagnetic spectrum. These sensors convert electromagnetic radiation into electrical signals that are in turn converted to digital values by a computer. These digital values can be used to construct an image.

Geographic information systems

Geographic information systems are computer-based systems that store, analyze, and display geographic information. Global positioning systems, remote sensing, and geographic information systems are increasingly valuable parts of the ecologist's tool kit.

Future avenues

Ecologists are using these new tools to study large-scale, dynamic ecological phenomena such as interannual variation in regional terrestrial primary production, dynamics of marine primary production, and potential population responses to climate change.

71-Competition

13.2 Failure of species to coexist in laboratory cultures led to the competitive exclusion principle

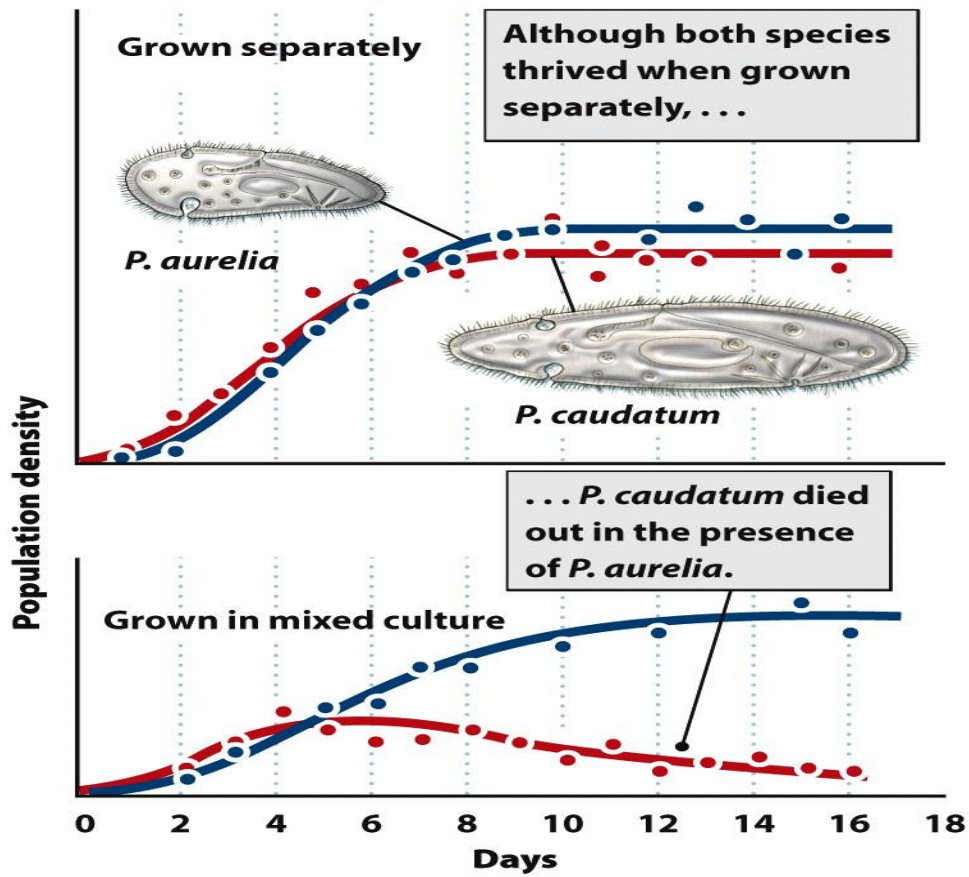


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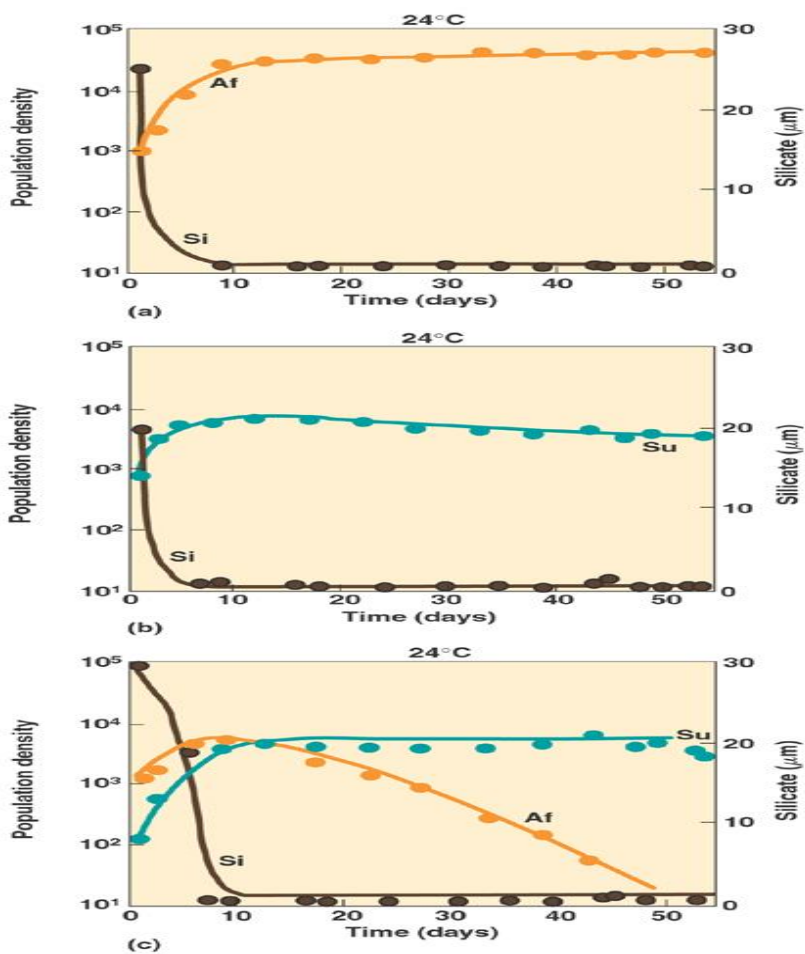
Diatom experiment

David Tilman, University of Minnesota

Asterionella formosa (Af) and *Synedra ulna* (Su) compete for silica for the formation of cell walls.

Grow well alone

Insufficient silica, Su reduced the silica to a low level and drove Af to extinction



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Competitive exclusion principle

- Principle: Complete competitors can not coexist. One species must go extinction
- Complete competitors: two species that live in the same place and possess exactly the same ecological requirements.
- Assumptions:
 - Exactly the same resource requirement (no more, no less)
 - Environmental conditions remain constant

72-Competition

13.4 Habitat productivity can influence competition between plant species

Two hypotheses:

1. Plants compete more intensively when mineral nutrients are less abundant in the soil (By Grubb and Tilman)

Plants compete more intensively when nutrients are less. High nutrients are less likely to limit plant population; thus the intraspecific competition is weak.

1. Competition is less intense when water and nutrients are less abundant (Grime and Keddy)

13.4 Habitat productivity can influence competition between plant species

Competition for light is more important than competition for nutrients; limit in water and nutrients would limit the population growth to a certain point that individual plants are widely spread and do not compete for light.

Difference between these hypotheses lies in the relative importance placed on belowground and aboveground competition for resources --Light or nutrient. (Debate)

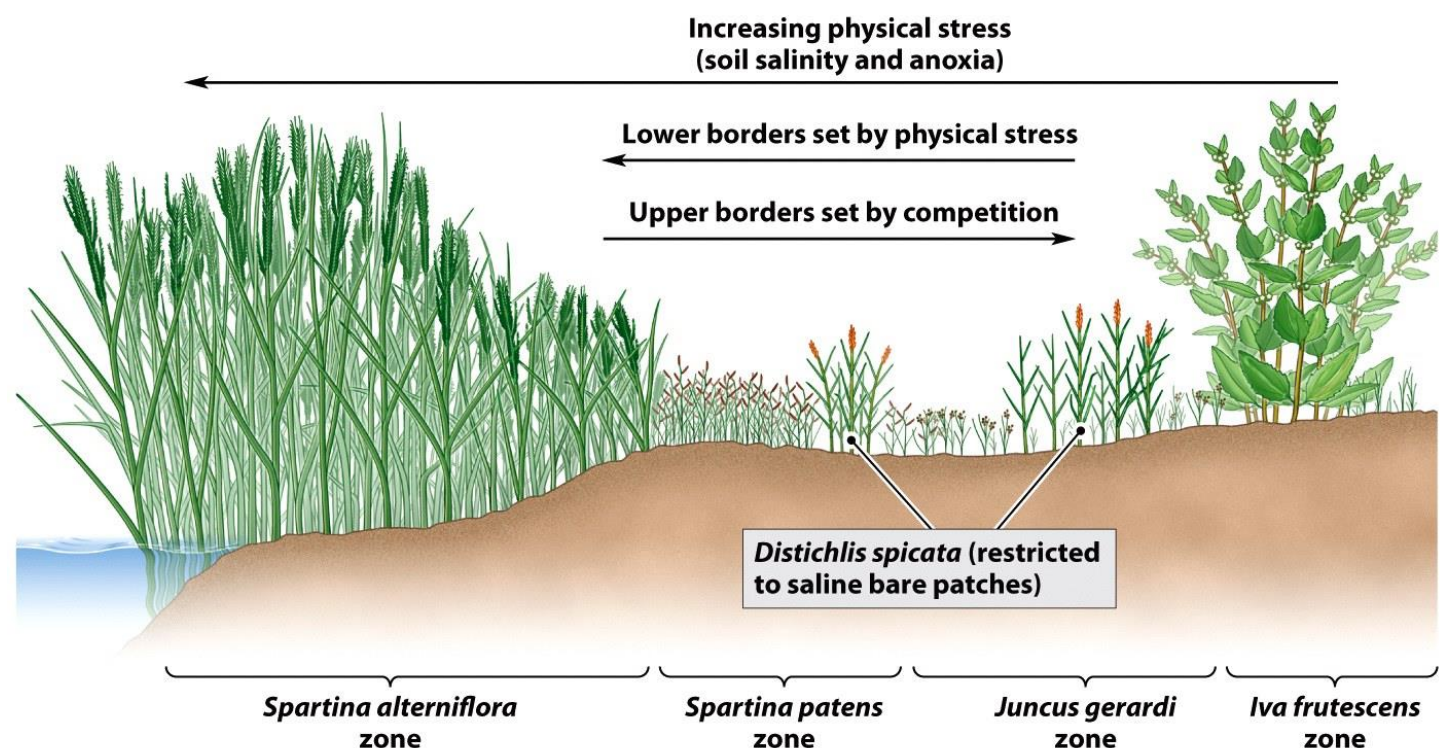


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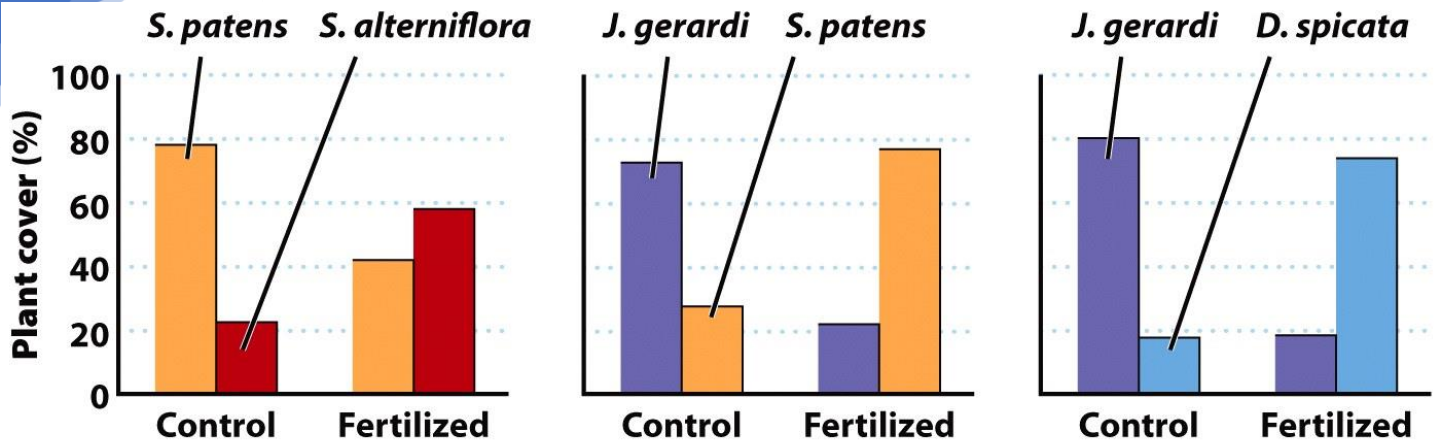


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Fertilization alters the outcome of competition by removing nutrient limitation on stress-tolerant plants, expand, away from water.

73-Competition

Interspecific competition reduces the equilibrium level of a population below the carrying capacity

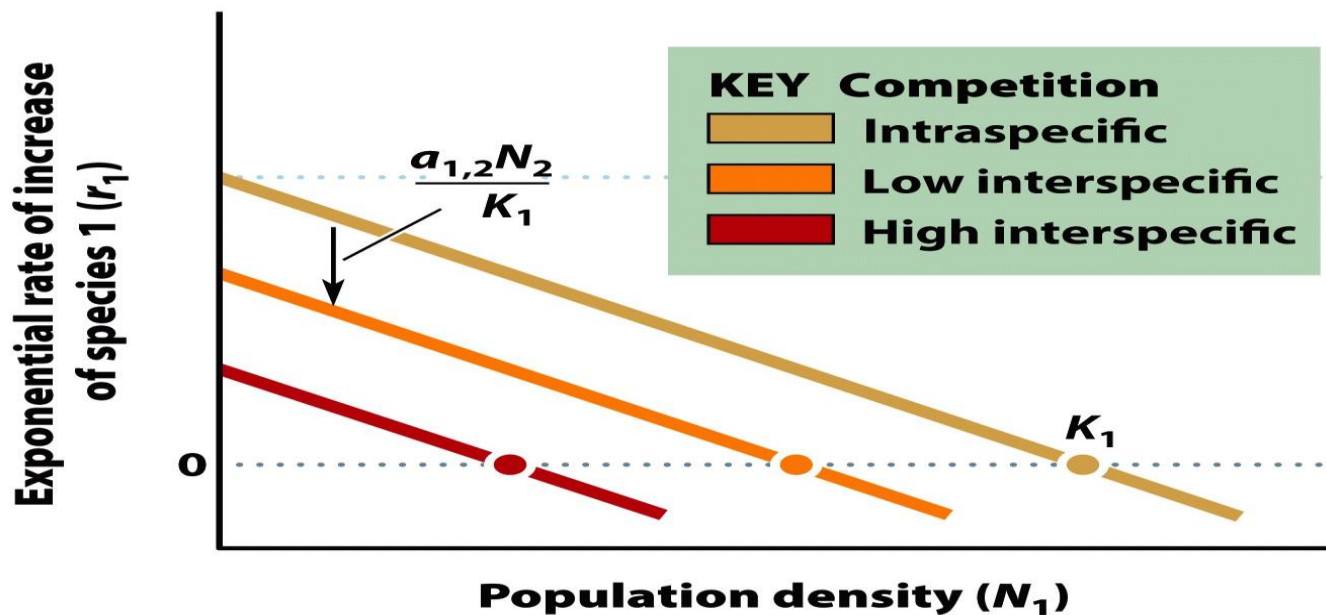


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There Are Four Possible Outcomes of Interspecific Competition

- In two situations, one of the species is the superior competitor and wins out over the other

A- In one case, species 1 inhibits the population of species 2 while continuing to increase

B- In one case, species 2 inhibits the population of species 1 while continuing to increase

(c) Species 1 inhibits growth of species 2 and latter goes extinction

(d) Species 2 inhibits growth of species 1 and latter goes extinction

There Are Four Possible Outcomes of Interspecific Competition

- In a third situation, each species, when abundant, inhibits the growth of the other (more than it inhibits its own growth)
 - Eventually one of the two species “wins”
- In a fourth situation, neither species eliminates the other resulting in coexistence
 - Each species inhibits its own population growth more than that of the other species

- (e) Unstable situation, both inhibit in a density dependent manner. Depending on initial density, either can make other extinct
- (f) Each species inhibits its own population growth more than competitor. Neither can eliminate competitor

74-Competition

13.5 Competition may occur through direct interference

- Exploitation: indirectly influencing each other by consuming the same resources (eat same grass by zebras , compete for water uptake by trees, indirectly)
- Interference: direct influencing each other by preventing others to occupy a habit or access resources

Consumers can influence the outcome of competition

Keystone predator

Starfish prey on mussels, barnacles, limpets, and chitons

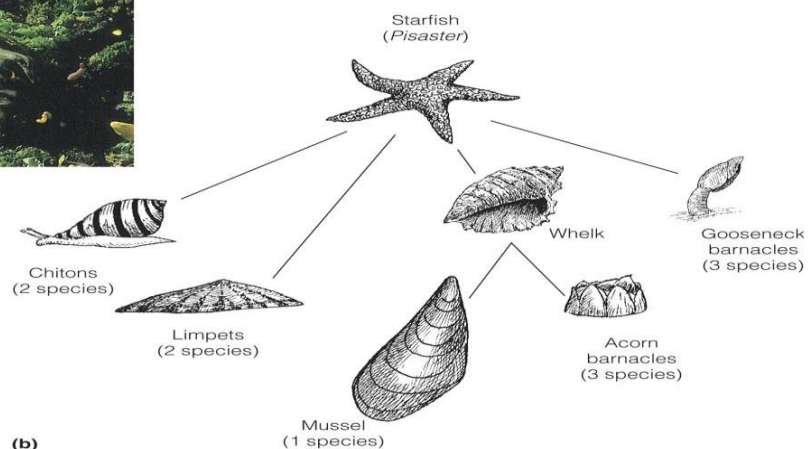
Remove starfish, what would happen?

Species diversity increase or decrease?

Why?



(a)

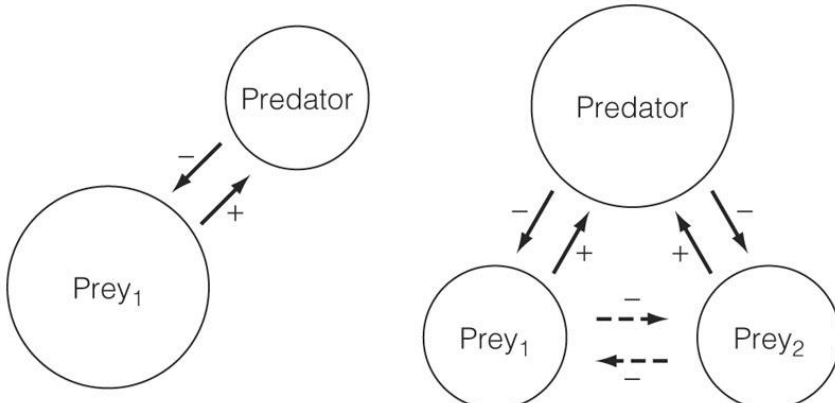


(b)

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Apparent competition

Combined populations of two prey species support a larger predator population neither can support alone. As a result, two prey populations reduced, gives outward appearance of interspecific competition.



(a)

(b)

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Apparent competition

- In the absence of predator, the population of each prey is regulated by purely intraspecific density-dependent mechanisms
- Neither prey species compete, directly or indirectly, with each other
- Predator abundance depends on the total abundance of prey
- Under these conditions, the combined population abundance of two prey species will support a higher predator density.

75-Energy and Nutrient Relations

Three main sources of energy

- Organisms use one of three main sources of energy:
 - light,
 - inorganic molecules, or
 - organic molecules.
- Photosynthetic plants and algae CO_2 as a source of carbon and light, of wavelengths between 400 and 700 nm, as a source of energy
- Light within this band, which is called photosynthetically active radiation, or PAR, accounts for about 45% of the total energy content of the solar spectrum at sea level.

PAR quantification

- PAR can be quantified as photosynthetic photon flux density, generally reported as μmol per square meter per second
- Among plants, there are three major alternative photosynthetic pathways, C_3 , C_4 , and CAM. C_4 and CAM plants are more efficient in their use of water than are C_3 plants.

Heterotrophs

- Heterotrophs use organic molecules both as a source of carbon and as a source of energy.
- Herbivores, carnivores, and detritivores face fundamentally different trophic problems.
- Herbivores feed on plant tissues. which often contain a great deal of carbon but little nitrogen.
- Herbivores must also overcome the physical and chemical defences of plants

76-Energy and Nutrient Relations

Detritivores

- Detritivores feed on dead plant material, which is even lower in nitrogen than living plant tissues
- Carnivores consume prey that are nutritionally rich but very well defended.
- Chemosynthetic autotrophs, which consist of a highly diverse group of chemosynthetic bacteria, use inorganic molecules as a source of energy
- Bacteria are the most tropically diverse organisms in the biosphere.

Rate of uptake of energy

- The rate at which organisms can take in energy is limited, either by external or internal constraints.
- The relationship between photon flux density and plant photosynthetic rate is called photosynthetic response.
- Herbs and short-lived perennial shrubs from sunny habitats have high maximum photosynthetic rates that level on at high light intensities.
- The lowest maximum rates of photosynthesis occur among plants from shady environments
- The relationship between food density and animal feeding rate is called the functional response.
- The shape of the functional response is generally one of three types.
- The forms of photosynthetic response curves and type 2 animal functional responses are remarkably similar

77-Rate of uptake of energy

Optimal foraging theory

- Optimal foraging theory attempts to model how organisms feed as an optimizing process.
- Evolutionary ecologists predict that if organisms have limited access to energy, natural selection is likely to favour individuals that are more effective at acquiring energy and nutrients.
- Many animals select food in a way that appears to maximize the rate at which they capture energy
- Plants appear to allocate energy to roots versus shoots in a way that increases their rate of intake of the resources that limit their growth.
- Plants in environments with abundant nutrients but little light tend to invest more energy in the growth of stems and leaves and less in roots.
- In environments rich in light but poor in nutrients, plants tend to invest more energy in the growth of roots.

Trophic diversity of bacteria

- The trophic diversity of bacteria, which is critical to the health of the biosphere, can also be used as a tool to address some of our most challenging waste disposal problems
- Bacteria can be used to eliminate the huge quantities of sewage produced by human populations, clean up soils and aquifers polluted by petroleum products such as benzene,
- And eliminate the pollution caused by some kinds of mine waste.

Role of bacteria

- The success of these projects requires that ecologists understand the energy and nutrient relations of bacteria.
- Bacteria will likely continue to play a great role as we address some of our most disturbing environmental problems.

78-Evaluating Molecular Homologies

- Systematics use computer programs and mathematical tools when analyzing comparable DNA segments from different organisms