40

Population Ecology and the Distribution of Organisms

Lecture Presentations by Kathleen Fitzpatrick and Nicole Tunbridge, Simon Fraser University
Discovering Ecology

- **Ecology** is the scientific study of the interactions between organisms and the environment.
- These interactions determine the distribution of organisms and their abundance.
- Modern ecology includes observation and experimentation.
Research questions an ecologist might ask following the discovery of a new species of frog include

- What environmental factors limit the geographic distribution of this species?
- How do interactions with other species affect population size?
Ecologists study interactions from the scale of individual organisms to the entire globe.
Global ecology

Landscape ecology

Ecosystem ecology

Community ecology

Population ecology

Organismal ecology

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• **Organismal ecology** considers how an organism’s structure, physiology, and behavior meet environmental challenges

• Organismal ecology includes physiological, evolutionary, and behavioral ecology
Figure 40.2-1

Organismal ecology
- **Population ecology** considers factors affecting population size over time.

- A **population** is a group of individuals of the same species living in an area.
Population ecology
Community ecology considers the whole array of interacting species in a community.

A community is a group of populations of different species in an area.
Community ecology
- **Ecosystem ecology** emphasizes energy flow and chemical cycling among the various biotic and abiotic components of the environment.

- An **ecosystem** is the community of organisms in an area and the physical factors with which they interact.
Ecosystem ecology
- **Landscape ecology** focuses on the exchanges of energy, materials, and organisms across multiple ecosystems.
- A **landscape** (or seascape) is a mosaic of connected ecosystems.
Landscape ecology
Global ecology is concerned with the biosphere, or global ecosystem, which is the sum of all the planet’s ecosystems.

Global ecology examines the influence of energy and materials on organisms across the biosphere.
Global ecology
Concept 40.1: Earth’s climate influences the distribution of terrestrial biomes

- The long-term prevailing weather conditions in an area constitute its **climate**
- Four major physical components of climate are temperature, precipitation, sunlight, and wind
- **Abiotic** factors are the nonliving chemical and physical attributes of the environment.
- **Biotic** factors are the other organisms that make up the living component of the environment.
Global Climate Patterns

- Global climate patterns are determined largely by solar energy and the planet’s movement in space.
- The warming effect of the sun causes temperature variations, which drive evaporation and the circulation of air and water.
- This causes latitudinal variations in climate.
Latitudinal variation in sunlight intensity is caused by the curved shape of Earth.

Sunlight strikes the tropics, regions between 23.5° north and 23.5° south latitude, most directly.

At higher latitudes, where sunlight strikes Earth at an oblique angle, light is more diffuse.
Atmosphere

Low angle of incoming sunlight

Sun overhead at equinoxes

Low angle of incoming sunlight

90°N (North Pole)

23.5°N (Tropic of Cancer)

0° (Equator)

23.5°S (Tropic of Capricorn)

90°S (South Pole)
- Global air circulation and precipitation patterns are initiated by intense solar radiation near the equator
- Warm, wet air rising near the equator creates precipitation in the tropics
- Dry air descending at 30° north and south latitudes causes desert conditions
- This pattern of precipitation and drying is repeated at the 60° north and south latitudes and the poles
66.5°N (Arctic Circle)

60°N

30°N

Westerlies

Northeast trades

0°

30°S

Westerlies

60°S

66.5°S (Antarctic Circle)

Descending dry air absorbs moisture.

Ascending moist air releases moisture.

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Figure 40.3-2a

66.5°N (Arctic Circle)

60°N

30°N

Westerlies

Northeast trades

0°

Southeast trades

30°S

Westerlies

60°S

66.5°S (Antarctic Circle)
Variation in the speed of Earth’s rotation at different latitudes results in the major wind patterns.

- Trade winds blow east to west in the tropics.
- Westerlies blow west to east in temperate zones.
Descending dry air absorbs moisture.

Ascending moist air releases moisture.
Regional Effects on Climate

- Climate is affected by seasonality, large bodies of water, and mountains
**Seasonality**

- Seasonal variations of light and temperature increase steadily toward the poles.
- Seasonality at high latitudes is caused by the tilt of Earth’s axis of rotation and its annual passage around the sun.
- Belts of wet and dry air straddling the equator shift throughout the year with the changing angle of the sun.
- Changing wind patterns affect ocean currents.
March equinox

June solstice

Constant tilt of 23.5°

December solstice

September equinox

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Bodies of Water

- Oceans, their currents, and large lakes moderate the climate of nearby terrestrial environments
- The California Current carries cold water southward along western North America
- The Gulf Stream carries warm water from the equator to the North Atlantic
During the day, air rises over warm land and draws a cool breeze from the water across the land.

As the land cools at night, air rises over the warmer water and draws cooler air from land back over the water, which is replaced by warmer air from offshore.
Mountains

- Rising air releases moisture on the windward side of a peak and creates a “rain shadow” as it absorbs moisture on the leeward side.
- Many deserts are found in the “rain shadow” of mountains.
Figure 40.6

Air flow

Windward side of mountains

Mountain range

Leeward side of mountains

Ocean
- Mountains affect the amount of sunlight reaching an area.
- In the Northern Hemisphere, south-facing slopes receive more sunlight than north-facing slopes.
- Every 1,000-m increase in elevation produces a temperature drop of approximately 6°C.
Climate and Terrestrial Biomes

- **Biomes** are major life zones characterized by vegetation type (terrestrial biomes) or physical environment (aquatic biomes)
- Climate determines vegetation type and limits the distribution of terrestrial biomes
- Latitudinal patterns in terrestrial biomes reflect the latitudinal patterns of climate
A **climograph** plots the annual mean temperature and precipitation in a region.

Biomes are affected not just by average temperature and precipitation, but also by the pattern of temperature and precipitation through the year.
Figure 40.8

Annual mean temperature (°C)

Annual mean precipitation (cm)

Desert
Temperate grassland
Temperate broadleaf forest
Tropical forest
Northern coniferous forest
Arctic and alpine tundra
Natural and human-caused disturbances alter the distribution of biomes

A disturbance is an event that changes a community by removing organisms and altering resource availability

- For example, frequent fires kill woody plants and can prevent savanna from transitioning into woodland
General Features of Terrestrial Biomes

- Terrestrial biomes are often named for major physical or climatic factors and for vegetation.
- Vertical layering is an important feature of terrestrial biome
- In a forest it might consist of an upper canopy, low-tree layer, shrub understory, ground layer of herbaceous plants, forest floor, and root layer
- Layering of vegetation provides diverse habitats for animals
- Terrestrial biomes usually grade into each other, without sharp boundaries.
- The area of intergradation, called an **ecotone**, may be wide or narrow.
Major features of terrestrial biomes include their global distribution, mean annual temperature and precipitation, and the dominant plants and animals.
- **Tropical forest** occurs in equatorial and subequatorial regions.
- Temperature is high year-round (25–29°C) with little seasonal variation.
- In **tropical rain forests**, rainfall is relatively constant, while in **tropical dry forests** precipitation is seasonal.
A tropical rain forest in Costa Rica
Tropical forests are vertically layered, and competition for light is intense.

Tropical forests are home to millions of animal species, including millions of undescribed species of arthropods.

Rapid human population growth is now destroying many tropical forests.
- **Savanna** occurs in equatorial and subequatorial regions
- Precipitation is seasonal
- Temperature averages 24–29°C but is more seasonally variable than in the tropics
A savanna in Kenya
- Grasses and forbs make up most of the ground cover.
- The dominant plant species are fire-adapted and tolerant of seasonal drought.
- Common inhabitants include insects and mammals such as wildebeests, zebras, lions, and hyenas.
- Fires set by humans may help maintain this biome.
Deserts occur in bands near 30° north and south of the equator and in the interior of continents.

Precipitation is low and highly variable, generally less than 30 cm per year.

Deserts may be hot (>50°C) or cold (−30°C) with seasonal and daily temperature variation.
Organ Pipe Cactus National Monument, Arizona
Desert plants are adapted for heat and desiccation tolerance, water storage, reduced leaf surface area, and defense from herbivores.

Common desert animals include scorpions, ants, beetles, snakes, lizards, migratory and resident birds, and seed-eating rodents; many are nocturnal.

Urbanization and conversion to irrigated agriculture have reduced the natural biodiversity of some deserts.
- **Chaparral** occurs in midlatitude coastal regions on several continents
- Precipitation is highly seasonal with rainy winters and dry summers
- Summer is hot (30°C); fall, winter, and spring are cool (10–12°C)
An area of chaparral in California
The chaparral is dominated by shrubs and small trees; many plants are adapted to fire and drought.

Animals include browsing mammals, insects, amphibians, small mammals, and birds.

Humans have reduced chaparral areas through agriculture and urbanization.
- **Temperate grasslands** occur at mid-latitudes, often in the interior of continents.
- Precipitation is highly seasonal.
- Winters are cold (often below $-10^\circ C$) and dry; summers are hot (often near $30^\circ C$) and wet.
A grassland in Mongolia
- The dominant plants, grasses and forbs, are adapted to droughts and fire
- Native mammals include large grazers such as bison and wild horses and small burrowers such as prairie dogs
- Most grasslands have been converted to farmland
- **Northern coniferous forest**, or taiga, spans northern North America and Eurasia and is the largest terrestrial biome on Earth
- Precipitation ranges from 30–70 cm
- Winters are cold; summers may be hot (e.g., Siberia ranges from −50°C to 20°C)
A coniferous forest in Norway
- Conifers such as pine, spruce, fir, and hemlock dominate
- Animals include migratory and resident birds and large mammals such as moose, brown bears, and Siberian tigers
- Periodic insect outbreaks kill vast tracts of trees
- Some forests are being logged at an alarming rate
■ Temperate broadleaf forest is found at midlatitudes in the Northern Hemisphere, with smaller areas in Chile, South Africa, Australia, and New Zealand

■ Significant amounts of precipitation fall during all seasons as rain or snow

■ Winters average 0°C; summers are hot and humid (near 35°C)
A temperate broadleaf forest in New Jersey
- Dominant plants include deciduous trees in the Northern Hemisphere and evergreen eucalyptus in Australia.
- In the Northern Hemisphere, many mammals hibernate in the winter; birds migrate to warmer areas.
- These forests have been heavily settled on all continents but are recovering in places.
- **Tundra** covers expansive areas of the Arctic; alpine tundra exists on high mountaintops at all latitudes.
- Precipitation is low in arctic tundra and higher in alpine tundra.
- Winters are cold (below \(-30^{\circ}\)C); summers are relatively cool (less than \(10^{\circ}\)C).
Dovrefjell-Sunndalsfjella National Park, Norway
Vegetation is herbaceous (mosses, grasses, forbs, dwarf shrubs, trees, and lichen)

Permafrost, a permanently frozen layer of soil, restricts growth of plant roots

Mammals include musk oxen, caribou, reindeer, bears, wolves, and foxes; many migratory bird species nest in the summer

Settlement is sparse, but tundra has become the focus of oil and mineral extraction
Concept 40.2: Aquatic biomes are diverse and dynamic systems that cover most of Earth

- Aquatic biomes are characterized primarily by their physical and chemical environment
  - For example, marine biomes have saltwater concentrations that average 3%, whereas freshwater biomes have salt concentrations of less than 0.1%
Aquatic biomes are stratified into vertical and horizontal zones.

Light is absorbed by water and photosynthetic organisms, so its intensity decreases rapidly with depth.

The upper **photic zone** has sufficient light for photosynthesis, while the lower **aphotic zone** receives little light.
- The photic and aphotic zones together make up the pelagic zone.
- The organic and inorganic sediment at the bottom of the pelagic zone is called the benthic zone.
- The communities of organisms in the benthic zone are collectively called the benthos.
In lakes, the aquatic biomes can be divided horizontally into the littoral zone and the limnetic zone

- **The littoral zone** includes waters close to shore that are shallow enough for rooted plants
- **The limnetic zone** includes waters farther from shore that are too deep to support rooted plants
In oceans and most lakes, a temperature boundary called the **thermocline** separates the warm upper layer from the cold deeper water.
Aquatic biomes show less latitudinal variation than terrestrial biomes

The largest marine biome is made of oceans, which cover about 75% of Earth’s surface and have an enormous impact on the biosphere
Aquatic communities are distributed according to water depth, degree of light penetration, distance from shore, and whether they are found in open water or near the bottom.
Major features of aquatic biomes include their physical and chemical environment, geological features, photosynthetic organisms, and heterotrophs.
- Wetlands and estuaries are among the most productive habitats on Earth
- Wetlands are inundated by water at least sometimes and support plants adapted to water-saturated soil
- An estuary is a transition area between river and sea; salinity varies with the rise and fall of the tides
- High organic production and decomposition in these biomes result in low levels of dissolved oxygen
A basin wetland in the United Kingdom
- Wetlands can develop in shallow basins, along flooded river banks, or on the coasts of large lakes
- Estuaries include a complex network of tidal channels, islands, and mudflats
- Plants are adapted to growing in periodically anaerobic, water-saturated soils
- Wetland plants include cattails and sedges; estuaries are characterized by saltmarsh grasses
- Wetlands are home to diverse invertebrates and birds, as well as frogs and alligators
- Estuaries support an abundance of marine invertebrates and fish consumed by humans
- Humans activities have destroyed up to 90% of wetlands and disrupted estuaries worldwide
- **Lakes** vary in size from a few square meters to thousands of square kilometers.
- Temperate lakes may have a seasonal thermocline; tropical lowland lakes have a year-round thermocline.
- **Oligotrophic lakes** are nutrient-poor and generally oxygen-rich.
- **Eutrophic lakes** are nutrient-rich and often depleted of oxygen.
An oligotrophic lake in Alberta, Canada
- Rooted and floating plants live in the littoral zone
- The limnetic zone is inhabited by phytoplankton and zooplankton, small drifting heterotrophs
- Invertebrates live in the benthic zone
- Fishes live in all zones with sufficient oxygen
- Human-induced nutrient enrichment can lead to algal blooms, oxygen depletion, and fish kills
- **Streams and rivers** have varying environmental conditions from headwater to mouth
- Headwater streams are generally cold, clear, turbulent, swift, and oxygen-rich; they are often narrow and rocky
- Downstream waters form rivers and are generally warmer and more turbid; they are often wide and meandering and have silty bottoms
- Salt and nutrients increase from headwaters to mouth; oxygen content decreases from headwaters to mouth
A headwater stream in Washington
• Headwater streams may be rich in phytoplankton or rooted aquatic plants
• A diversity of fishes and invertebrates inhabit unpolluted rivers and streams
• Pollution degrades water quality and kills aquatic organisms
• Dams impair natural flow of stream and river ecosystems
- **Intertidal zones** are periodically submerged and exposed by the tides
- Intertidal organisms are challenged by variations in temperature and salinity and by the mechanical forces of wave action
- Oxygen and nutrient levels are high
- Substrate may be rocky or sandy
A rocky intertidal zone on the Oregon coast
- Protected sandy zones support sea grass and algae; rocky zones support attached marine algae.
- In rocky zones, many animals have structural adaptations for attaching to rock.
- In sandy zones, worms, clams, and crustaceans bury themselves in sand.
- Other animals include sponges, sea anemones, and small fishes.
- Oil pollution has disrupted many intertidal areas.
- **Coral reefs** are formed from the calcium carbonate skeletons of corals.

- Shallow reef-building corals live in the photic zone in warm (about 20–30°C), clear water; deep-sea corals live at depths of 200–1,500 m.

- Corals require high oxygen concentrations and a solid substrate for attachment.

- A coral reef progresses from a fringing reef to a barrier reef to a coral atoll.
A coral reef in the Red Sea
Corals are the predominant animals on the reef. They form mutualisms with symbiotic algae that provide them organic molecules. A high diversity of fish and invertebrates inhabit coral reefs. Coral collection, overfishing, global warming, and pollution all contribute to reduction in coral populations.
The **oceanic pelagic zone** is constantly mixed by wind-driven oceanic currents.

- Oxygen levels are high.
- Turnover in temperate oceans renews nutrients in the photic zones.
- This biome covers approximately 70% of Earth’s surface.
Open ocean near Iceland
- Phytoplankton are the dominant photosynthetic organisms
- Zooplankton including protists, worms, krill, jellies, and invertebrate larvae feed on the phytoplankton
- Free-swimming animals include squids, fishes, sea turtles, and marine mammals
- Overfishing has depleted fish stocks
- Humans have polluted oceans with dumping of waste
• The **marine benthic zone** consists of the seafloor
• Organisms in the very deep benthic (abyssal) zone are adapted to continuous cold and high water pressure
• Substrate is mainly soft sediments; some areas are rocky
• Shallow areas contain seaweeds and filamentous algae

• In dark, hot environments near deep-sea hydrothermal vents of volcanic origin, the food producers are chemoautotrophic prokaryotes

• Giant tube worms, arthropods, and echinoderms are abundant heterotrophs near hydrothermal vents
A deep-sea hydrothermal vent community
Coastal benthic communities include invertebrates and fishes

Overfishing and dumping of organic waste have depleted fish populations
Concept 40.3: Interactions between organisms and the environment limit the distribution of species

- Species distributions are a consequence of both ecological factors and evolutionary history.
- Geographic isolation can result in the evolution of unique lineages restricted to specific areas.
  - For example, the kangaroo lineage occurs only on the isolated continent of Australia.
Ecologists ask questions about where species occur and why they occur where they do.

Ecological factors including food availability, predators, and temperature can influence the movement of species outside of their native range.
Why is species X absent from an area?

Does dispersal limit its distribution?

Yes

Area inaccessible or insufficient time

No

Do biotic factors (other species) limit its distribution?
Why is species X absent from an area?

- Does dispersal limit its distribution?
  - Yes -> Area inaccessible or insufficient time
  - No

- Do biotic factors (other species) limit its distribution?
  - Yes
  - No -> Predation, parasitism, competition, disease

- Do abiotic factors limit its distribution?
Why is species X absent from an area?

Does dispersal limit its distribution?

Do biotic factors (other species) limit its distribution?

Do abiotic factors limit its distribution?

Chemical factors
- Water, oxygen, salinity, pH, soil nutrients, etc.

Physical factors
- Temperature, light, soil structure, fire, moisture, etc.

Predation, parasitism, competition, disease
Dispersal and Distribution

- **Dispersal** is the movement of individuals away from centers of high population density or from their area of origin.
- Dispersal contributes to the global distribution of organisms.
Transplants indicate if dispersal is a key factor limiting species distributions.

Transplants include organisms that are intentionally or accidentally relocated from their original distribution.

If a transplant is successful, it indicates that the species’ potential range is larger than its actual range.

Species transplants can disrupt the communities or ecosystems to which they have been introduced.
Biotic Factors

- Biotic factors that affect the distribution of organisms may include
  - Predation
  - Herbivory
  - Mutualism
  - Parasitism
  - Competition
- Sea urchins are important herbivores in marine ecosystems
- Feeding by sea urchins and, to a lesser degree, limpets can limit the distribution of seaweed
Results

Seaweed cover (%)

August 1982  |  February 1983  |  August 1983  |  February 1984

- **Sea urchin**: Both limpets and urchins removed
- **Limpet**: Only limpets removed
- **Control (both urchins and limpets present)**

Sea urchin
Figure 40.13-2

Limpet
Abiotic Factors

- Abiotic factors affecting the distribution of organisms include
  - Temperature
  - Water and oxygen
  - Salinity
  - Sunlight
  - Rocks and soil
- **Temperature** limits the distribution of organisms because of its effect on biological processes.
- Cells may freeze and rupture below 0°C, while most proteins denature above 45°C.
- Most organisms function best within a specific temperature range.
Availability of **water and oxygen** is an important factor in species distribution.

Terrestrial organisms face a constant threat of desiccation; their distribution reflects their ability to obtain and store water.

Oxygen can be limiting in some aquatic systems and soils because it diffuses slowly in water.
Salinity, salt concentration, affects the water balance of organisms through osmosis.

Most aquatic organisms are restricted to either freshwater or saltwater habitats.

Few terrestrial plants and animals are adapted to high-salinity habitats.
- **Sunlight** is the energy source for photosynthetic organisms and, as such, can limit their distribution.
- In aquatic environments, most photosynthesis occurs near the surface where sunlight is available.
- Shading by the canopy drives intense competition for light in forests.
- **Rocks and soil** can limit the distribution of organisms through their effects on the pH, mineral composition, and physical structure of the substrate.
Concept 40.4: Biotic and abiotic factors affect population density, dispersion, and demographics

- Population ecology explores how biotic and abiotic factors influence density, distribution, and size of populations
- A population is a group of individuals of a single species living in the same general area
- Populations are described by their boundaries and size
Density and Dispersion

- **Density** is the number of individuals per unit area or volume
- **Dispersion** is the pattern of spacing among individuals within the boundaries of the population
Density: A Dynamic Perspective

- In most cases, it is impractical or impossible to count all individuals in a population.
- Sampling techniques can be used to estimate densities and total population sizes.
- Population density can be estimated by extrapolation from small samples or an indicator of population size (for example, number of nests).
Density is the result of an interplay between processes that add individuals to a population and those that remove individuals.

- Additions occur through birth and immigration, the influx of new individuals from other areas.
- Removal of individuals occurs through death and emigration, the movement of individuals out of a population.
Births and immigration add individuals to a population.

Deaths and emigration remove individuals from a population.
Patterns of Dispersion

- Environmental and social factors influence the spacing of individuals in a population.
- The most common pattern of dispersion is clumped, in which individuals aggregate in patches.
- A clumped dispersion may be influenced by resource availability and behavior.
(a) Clumped

(b) Uniform

(c) Random
(a) Clumped  
(b) Uniform  
(c) Random
(a) Clumped
A uniform dispersion is one in which individuals are evenly distributed.

In plants, it may occur as a result of the secretion of chemicals that inhibit the growth or germination of nearby individuals.

In animals, it may be influenced by social interactions such as **territoriality**, the defense of a bounded space against other individuals.
(b) Uniform
In a random dispersion, the position of each individual is independent of other individuals.

- It occurs in the absence of strong attractions or repulsions among individuals.
- It can also occur where key physical or chemical factors are relatively constant across the study area.
(c) Random
Demographics

- **Demography** is the study of the vital statistics of a population and how they change over time.
- Death rates and birth rates are of particular interest to demographers.
**Life Tables**

- A **life table** is an age-specific summary of the survival pattern of a population.
- It is best made by following the fate of a **cohort**, a group of individuals of the same age, from birth to death.
- Life tables constructed for sexually reproducing species often ignore males because only females produce offspring.
Table 40.1 Life Table for Female Belding’s Ground Squirrels (Tioga Pass, in the Sierra Nevada of California)

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Number Alive at Start of Year</th>
<th>Proportion Alive at Start of Year†</th>
<th>Death Rate‡</th>
<th>Average Number of Female Offspring</th>
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<tbody>
<tr>
<td>0–1</td>
<td>653</td>
<td>1.000</td>
<td>0.614</td>
<td>0.00</td>
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<td>1–2</td>
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<td>1</td>
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<td>1.00</td>
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</tr>
</tbody>
</table>


†Indicates the proportion of the original cohort of 653 individuals that are still alive at the start of a time interval.

‡The death rate is the proportion of individuals alive at the start of a time interval that die during that time interval.
Survivorship Curves

- A **survivorship curve** is a graphic way of representing the data in a life table.
- Survivorship curves plot the proportion or numbers of a cohort still alive at each age.
Survivorship curves can be classified into three general types

- **Type I**: high survivorship during early and middle life followed by a steep drop due to increase in death rates among older age groups
- **Type II**: survivorship declines linearly due to a constant death rate over the organism’s life span
- **Type III**: low survivorship due to high death rates for young age-groups and stable survivorship later in life due to a lower death rate for survivors
Many species have survivorship curves intermediate to the three types described, while others show more complex patterns.
Reproductive Rates

- A reproductive table, or fertility schedule, is an age-specific summary of the reproductive rates in a population.
- Reproductive output is typically measured as the average number of female offspring for each female in a given age-group.
Concept 40.5: The exponential and logistic models describe the growth of populations

- Unlimited growth occurs under ideal conditions; in nature, growth is limited by various factors
- Ecologists study growth in both idealized and realistic conditions
Changes in Population Size

- Change in population size can be defined by the equation

\[
\text{Change in population size} = \text{Births entering population} - \text{Deaths} - \text{Emigrants leaving population} + \text{Immigrants entering population}
\]

- If immigration and emigration are ignored, the change in population size equals births minus deaths
The population growth rate can be expressed mathematically as

\[ \frac{\Delta N}{\Delta t} = B - D \]

where \( \Delta N \) is the change in population size, \( \Delta t \) is the time interval, \( B \) is the number of births, and \( D \) is the number of deaths in the population during the time interval.
The population growth equation can be revised

\[ \frac{\Delta N}{\Delta t} = R \]

where \( R \) represents the difference between the number of births \( (B) \) and the number of deaths \( (D) \).
The per capita (per individual) change in population size ($r_{\Delta t}$) represents the contribution that an average member of the population makes to the population size during the time interval $\Delta t$.

For example, for a population of 1,000 individuals that increases by 16 individuals per year,

$$r_{\Delta t} = \frac{16}{1,000} = 0.016$$
The formula $R = r_{\Delta t}N$ can be used to calculate how many individuals will be added to a population each year.

For example, if $r_{\Delta t} = 0.016$ and the population size is 500,

$$R = r_{\Delta t}N = 0.016 \times 500 = 8 \text{ per year}$$
Change in population size can now be written as

$$\frac{\Delta N}{\Delta t} = r_{\Delta t}N$$
Population growth can also be expressed as a rate of change at each instant in time:

\[
\frac{dN}{dt} = rN
\]

where \(\frac{dN}{dt}\) represents very small changes in population size over short (instantaneous) time intervals.
Exponential Growth

- **Exponential population growth** is population increase under idealized conditions (food is abundant and all individuals reproduce at physiological capacity)
- Under these conditions, the population increases in size by a constant proportion at each instant in time
The equation of exponential population growth is

\[
\frac{dN}{dt} = rN
\]

where \( r \) is the **intrinsic rate of increase**, the per capita rate at which a population increases in size at each instant in time.
- A population growing exponentially increases at a constant rate ($r$).
- This results in a J-shaped growth curve.
- A population with a higher intrinsic rate of increase will have a steeper growth curve.
Figure 40.17

\[ \frac{dN}{dt} = 1.0N \]

\[ \frac{dN}{dt} = 0.5N \]

Population size \( (N) \)

Number of generations

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The J-shaped curve of exponential growth characterizes populations in new environments or rebounding populations

- For example, the elephant population in Kruger National Park, South Africa, grew exponentially after hunting was banned
Carrying Capacity

- Exponential growth cannot be sustained for long in any population
- A more realistic population model limits growth by incorporating carrying capacity
- **Carrying capacity** \((K)\) is the maximum population size the environment can support
- Carrying capacity varies with the abundance of limiting resources
As a population approaches carrying capacity, the per capita birth rate will decrease or the per capita death rate will increase.

Such changes in either (or both) of these rates cause the per capita growth rate \((r)\) to drop.
The Logistic Growth Model

- In the **logistic population growth** model, the per capita rate of increase approaches zero as carrying capacity is reached.
- The logistic model starts with the exponential model and adds an expression that reduces per capita rate of increase as $N$ approaches $K$.

\[
\frac{dN}{dt} = rN \frac{(K - N)}{K}
\]
- Population growth is highest when the population size is at half the carrying capacity.
- At half carrying capacity the per capita rate of increase remains relatively high and there are more reproducing individuals than at low population size.
Table 4.2 Logistic Growth of a Hypothetical Population ($K = 1,500$)

<table>
<thead>
<tr>
<th>Population Size ($N$)</th>
<th>Intrinsic Rate of Increase ($r$)</th>
<th>$\frac{K - N}{K}$</th>
<th>$r \frac{(K - N)}{K}$</th>
<th>$rN \frac{(K - N)}{K}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>1.0</td>
<td>0.983</td>
<td>0.983</td>
<td>+ 25</td>
</tr>
<tr>
<td>100</td>
<td>1.0</td>
<td>0.933</td>
<td>0.933</td>
<td>+ 93</td>
</tr>
<tr>
<td>250</td>
<td>1.0</td>
<td>0.833</td>
<td>0.833</td>
<td>+ 208</td>
</tr>
<tr>
<td>500</td>
<td>1.0</td>
<td>0.667</td>
<td>0.667</td>
<td>+ 333</td>
</tr>
<tr>
<td>750</td>
<td>1.0</td>
<td>0.500</td>
<td>0.500</td>
<td>+ 375</td>
</tr>
<tr>
<td>1,000</td>
<td>1.0</td>
<td>0.333</td>
<td>0.333</td>
<td>+ 333</td>
</tr>
<tr>
<td>1,500</td>
<td>1.0</td>
<td>0.000</td>
<td>0.000</td>
<td>0</td>
</tr>
</tbody>
</table>

*Rounded to the nearest whole number.*
The logistic model of population growth produces a sigmoid (S-shaped) curve
Exponential growth

\[
\frac{dN}{dt} = 1.0N
\]

Logistic growth

\[
\frac{dN}{dt} = 1.0N \left(\frac{1,500 - N}{1,500}\right)
\]

Population size \((N)\)

Population growth begins slowing here.

\(K = 1,500\)

Number of generations
The Logistic Model and Real Populations

- The growth of many laboratory populations, including paramecia, fits an S-shaped curve when resources are limited.
- These organisms are grown in a constant environment lacking predators and competitors.
(a) A *Paramecium* population in the lab
The logistic model fits few real populations

Some populations overshoot $K$ before settling down to a relatively stable density

Some populations fluctuate greatly and make it difficult to define $K$
(b) A *Daphnia* (water flea) population in the lab
Figure 40.20

(a) A Paramecium population in the lab

(b) A Daphnia (water flea) population in the lab
Concept 40.6: Population dynamics are influenced strongly by life history traits and population density

- An organism’s **life history** comprises the traits that affect its schedule of reproduction and survival
  - The age at which reproduction begins
  - How often the organism reproduces
  - How many offspring are produced per reproductive episode
“Trade-offs” and Life Histories

- Organisms have finite resources, which may lead to trade-offs between survival and reproduction.
- Selective pressures influence the trade-off between the number and size of offspring.
- Plants and animals whose young are likely to die often produce large numbers of small offspring.
Some plants and animals produce a moderate number of large offspring.

For these species, extra investment by the parent greatly increases the offspring’s chance of survival.
(a) Dandelions release a large number of tiny fruits.

(b) The Brazil nut tree (above), produces a moderate number of large seeds in pods (left).
- **K-selection**, or density-dependent selection, operates in populations experiencing competitive conditions at population densities close to carrying capacity.

- **r-selection**, or density-independent selection, selects for life history traits that maximize reproduction at low population density.
Population Change and Population Density

- In **density-independent** populations, birth rate and death rate do not change with population density.
- In **density-dependent** populations, birth rates fall and death rates rise with population density.
When the density is low, there are more births than deaths. Hence, the population grows until the density reaches $Q$.

When the density is high, there are more deaths than births. Hence, the population shrinks until the density reaches $Q$.

Equilibrium density ($Q$)

Density-independent death rate

Density-dependent birth rate

Birth or death rate per capita

Population density
Mechanisms of Density-Dependent Population Regulation

- Density-dependent birth and death rates are an example of negative feedback that regulates population growth
- Population growth declines at high density due to factors such as competition for resources, predation, disease, toxic wastes, territoriality, and intrinsic factors
Competition for resources occurs in crowded populations; increasing population density intensifies competition for resources and results in a lower birth rate.
Competition for resources
- **Predation** may increase with increasing population size due to increased predator success at high density and preference for abundant prey species.
Predation
Disease transmission rates may increase with increasing population density
Disease
- **Toxic wastes** produced by a population can accumulate in the environment, contributing to density-dependent regulation of population size.
Toxic wastes
**Territoriality** can limit population density when space becomes a limited resource.
Territoriality
Intrinsic factors (physiological factors) such as hormonal changes appear to regulate population size in some species.
Intrinsic factors
Population Dynamics

- The study of population dynamics focuses on the complex interactions between biotic and abiotic factors that cause variation in population size.
Stability and Fluctuation

- Long-term population studies have challenged the hypothesis that populations of large mammals are relatively stable over time.

- Both weather and predator population can affect population size over time.
  - For example, collapses in the moose population on Isle Royale coincided with a peak in the wolf population during one time period and with harsh winter conditions in another.
\[
\frac{dN}{dt} = rN
\]
Metapopulations are groups of populations linked by immigration and emigration

Local populations within a metapopulation occupy patches of suitable habitat surrounded by unsuitable habitat

Populations can be replaced in patches after extinction or established in new unoccupied habitats through migration
Figure 40.23

Competition for resources
Predation
Disease
Toxic wastes
Territoriality
Intrinsic factors
### Table 40.2  Logistic Growth of a Hypothetical Population (K = 1,500)

<table>
<thead>
<tr>
<th>Population Size (N)</th>
<th>Intrinsic Rate of Increase (r)</th>
<th>$\frac{K - N}{K}$</th>
<th>$r \frac{(K - N)}{K}$</th>
<th>Population Growth Rate*</th>
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</tbody>
</table>

*Rounded to the nearest whole number.
Daphnia
Population size ($N$)

$K = \text{carrying capacity}$

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

Number of generations