

## 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 and island isolation

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

- time since perturbation,
- productivity,
- environmental heterogeneity,
- favorableness,
- niche breadths and interspecific interactions, and
- 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.

## 45 Evidence for evolution

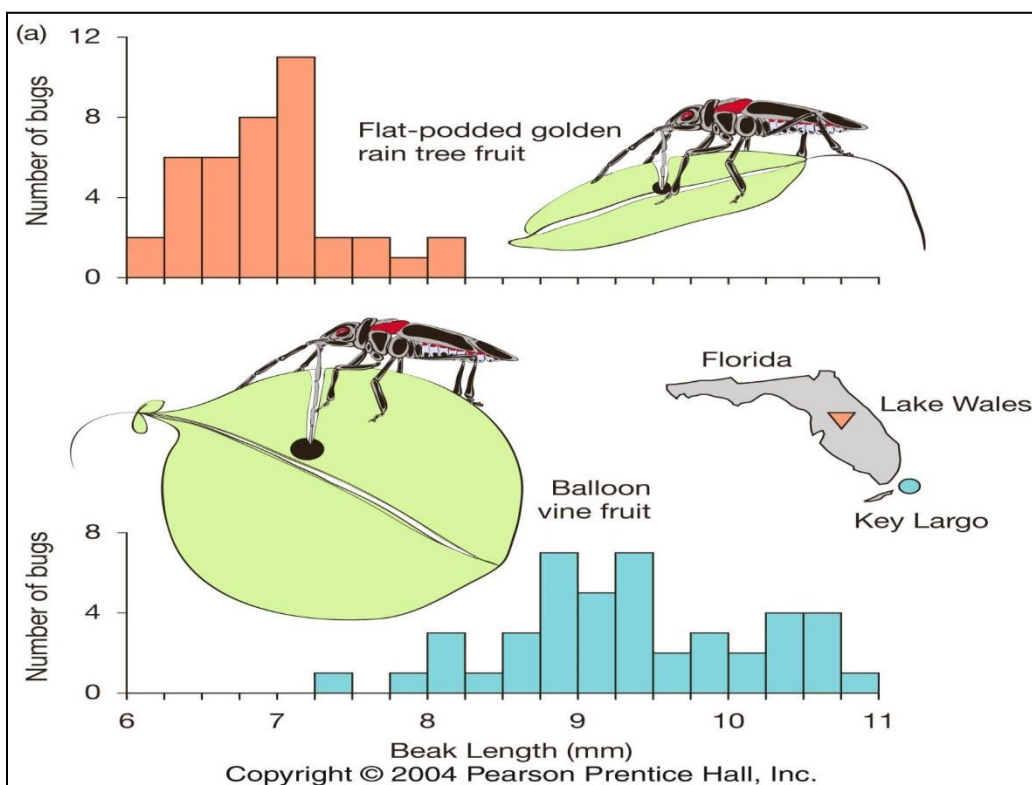
### Darwin's Theory of Evolution by Natural Selection

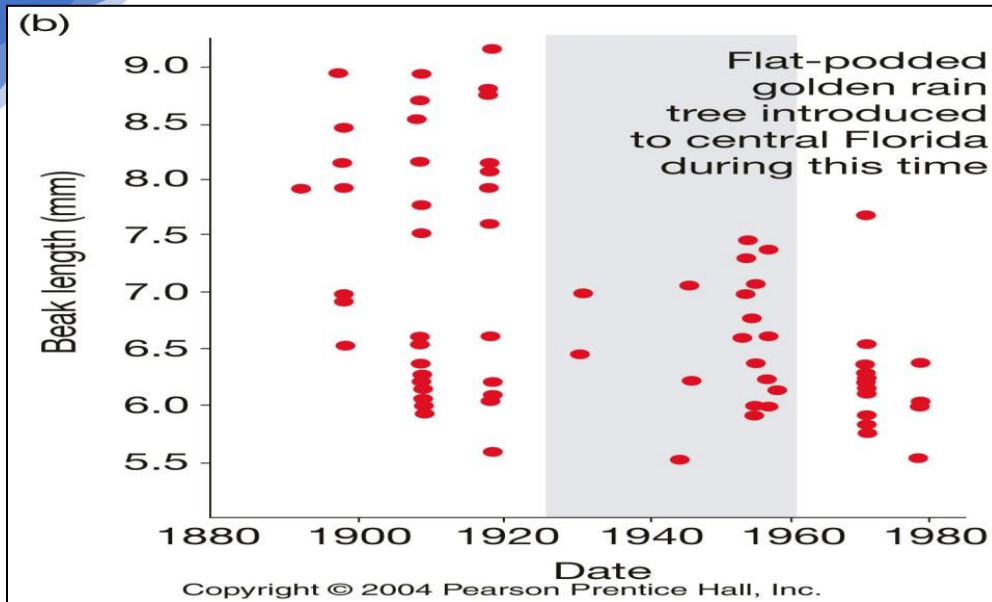
- Species have changed through time and are related by descent from a common ancestor
- The primary mechanism of Evolutionary Change is Natural Selection

### Evidence that Species have Changed Through Time?

- **Hypothesis:** Species have changed through time
- **Prediction:** we should be able to find signs of evolutionary history
  - direct observation
  - fossil record
  - vestigial structures

Direct observation of Evolution





## Fossil Record

The fossil record is the history of life recorded by remains from the past. Most fossils are at least 10,000 years old.

1. Body Fossil
2. Trace Fossil

## What is found?

- Fossils exist and fossil forms are unlike species living today

### 1. Fossil Sequence?

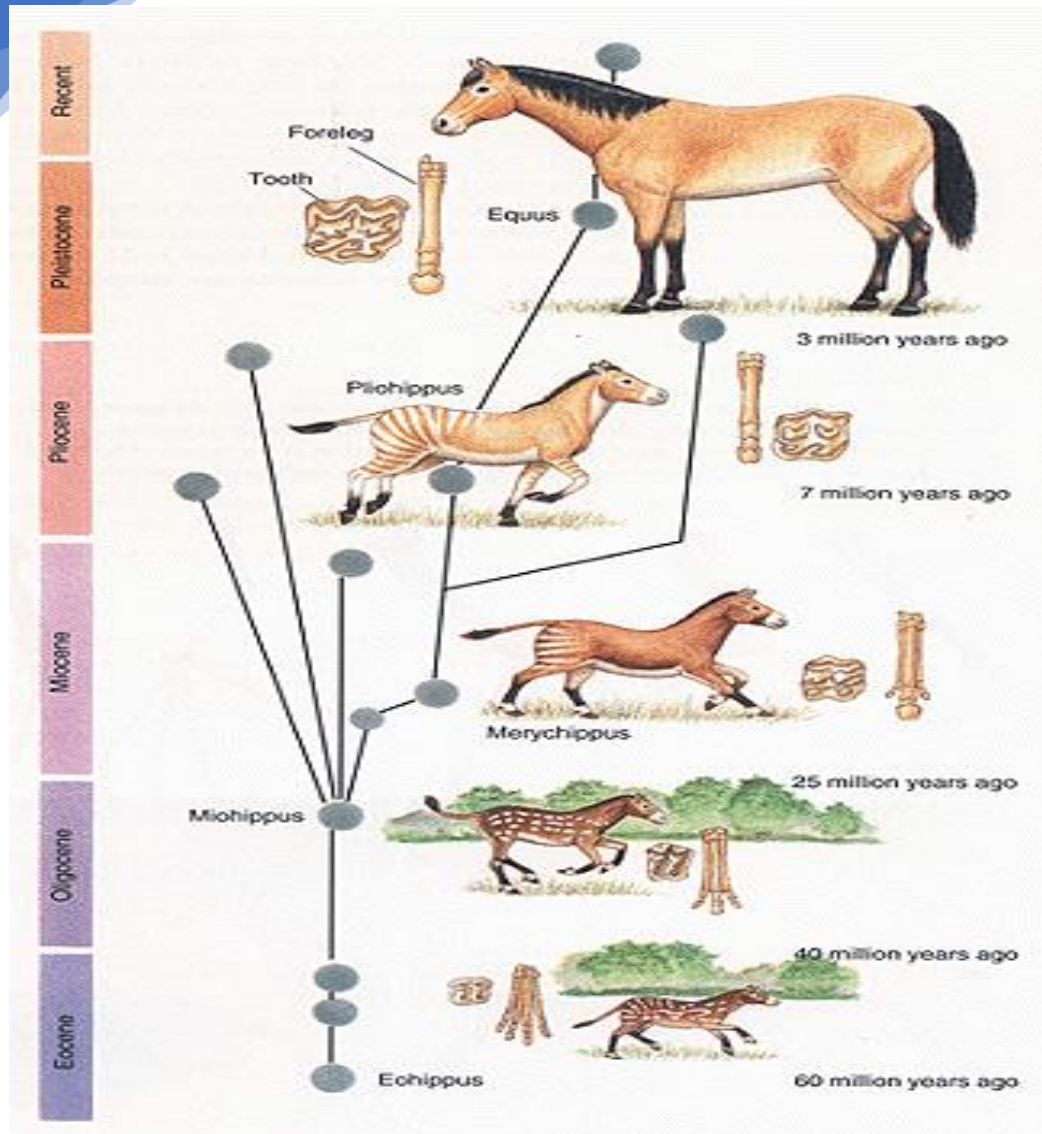
When fossils are arranged according to their age, they show successive evolutionary change

### 2. Fossil Intermediates?

Transitional fossils have been found between: Amphibians & reptiles, reptiles & birds, reptiles & mammals, apes and humans

## The Evolution of Horses

A particularly well-documented case of evolution within a group



### The fossil Record is Incomplete

At the time of Darwin, the fossil record was VERY scanty. A great deal of progress has been made since, but it is far from finished.

### The fossil record is relatively incomplete for several reasons:

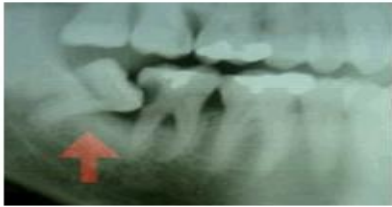
1. Soft tissues are rarely preserved
2. Movement of the earth's crust has obliterated and/or covered many fossils
3. Fossilization takes place only in certain types of habitats and favorable environments
4. Paleontologists have not dug up every place on earth

**Even if there were no fossil record, the evidence from living organisms would be more than sufficient to demonstrate the historical reality of evolution**

### Vestigial Structures

- Features that have no apparent function
- Typically have an important function in related spp.
- Ex: Hindlimb joints in whales and snakes
- In humans Wisdom teeth, Tail bone, Appendix are vestigial structures.

## Vestigial Structures in Humans



Wisdom Teeth

Tailbone

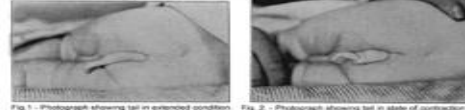
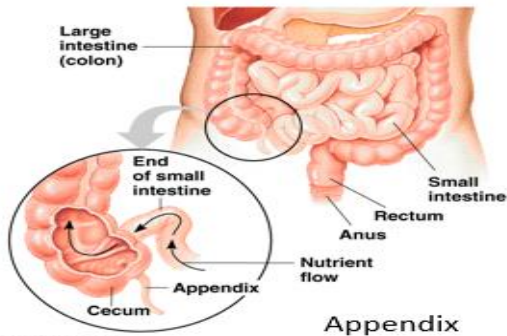
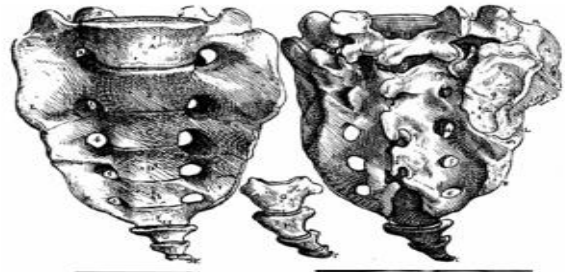


Fig. 1 - Photograph showing tail in extended condition Fig. 2 - Photograph showing tail in state of contraction



### Evidence for the Relatedness of Life Forms?

- Hypothesis: all living organisms have descended from a common ancestor
- Prediction: we should also be able to see evidence of relatedness of species
  - Homology
  - Geographic distribution

#### Homology:

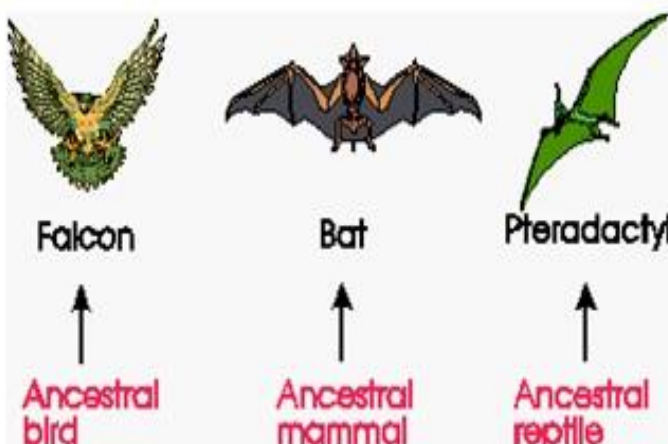
- Homology: a similarity between species that is the result from the inheritance of traits from a common ancestor
- The features of every creature reflect history as well as adaptation

#### 3 types of homologies

- structural
- developmental
- genetic

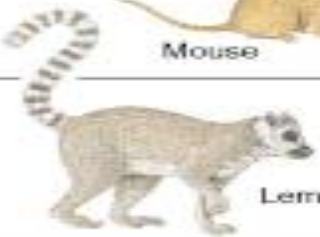
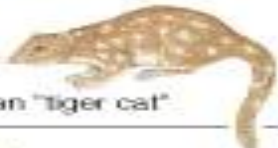
#### Homology vs. Analogy:

Natural selection appears to have favored similar adaptations in unrelated organisms in similar environments--> these structures are **analogous**

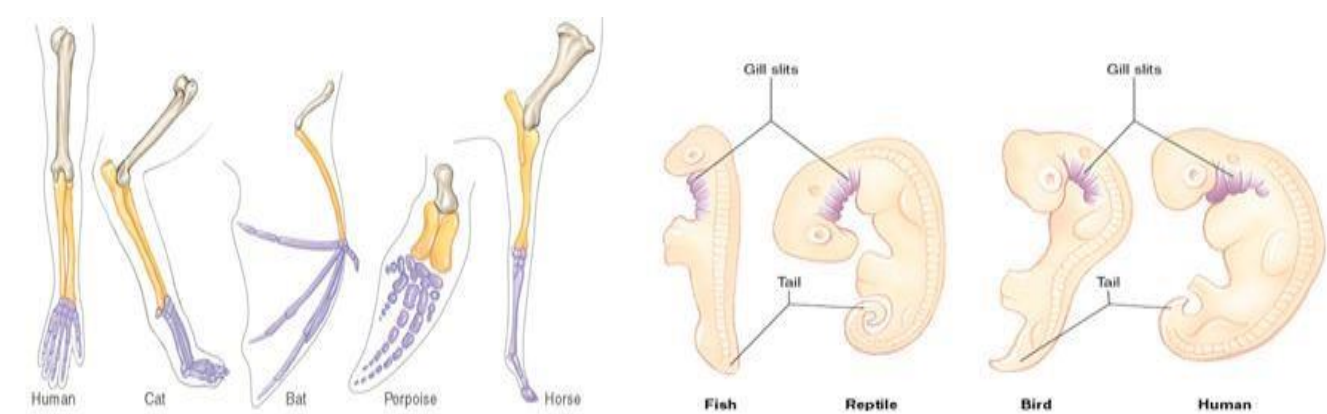


Whereas homologous structures share structural similarity, but not function, analogous structures share function but not structural similarity since they evolved independently

#### Convergent Evolution

| Niche    | Placental Mammals                                                                                 | Australian Marsupials                                                                                      |
|----------|---------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------|
| Burrower |  Mole            |  Marsupial mole          |
| Anteater |  Anteater        |  Numbat (anteater)      |
| Mouse    |  Mouse           |  Marsupial mouse         |
| Climber  |  Lemur           |  Spotted cuscus          |
| Glider   |  Flying squirrel |  Flying phalanger       |
| Cat      |  Bobcat         |  Tasmanian "tiger cat" |
| Wolf     |  Wolf          |  Tasmanian wolf        |

Homologous structures: bones of the forelimb:



The underlying design of each structure is similar despite their functional differences

Homologous structures in adults develop from homologous groups of cells in embryos --> they share developmental pathways

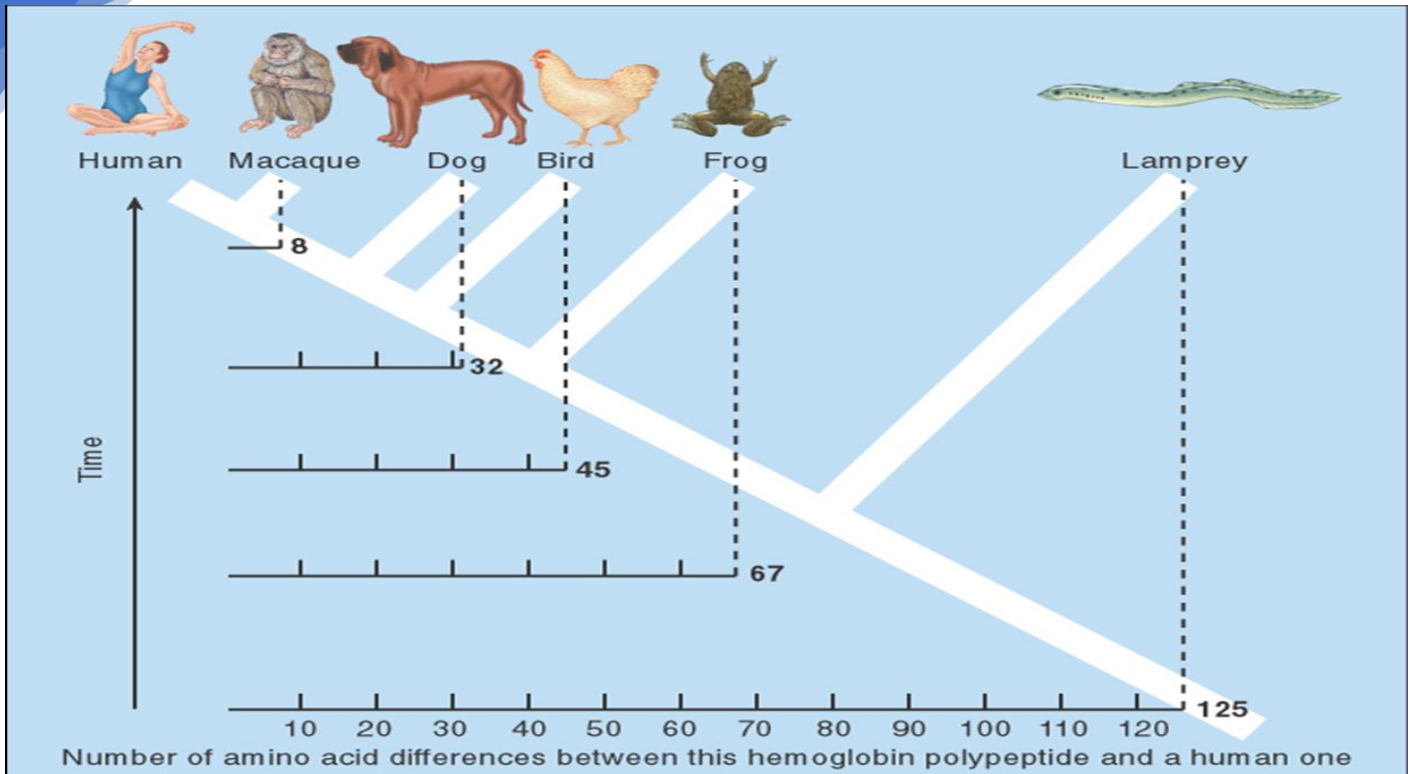
Convergent Evolution:

**Convergent evolution** is the process by which unrelated or distantly related organisms **evolve** similar body forms, coloration, organs, and adaptations. Natural selection can result in **evolutionary convergence** under several different circumstances.

Genetic Homologies

All living organisms share the same genetic code. Chromosome and gene similarities between species match evolutionary similarities. This is true for both coding regions and "junk DNA"

Molecules reflect evolutionary divergence



### Geographic Distributions

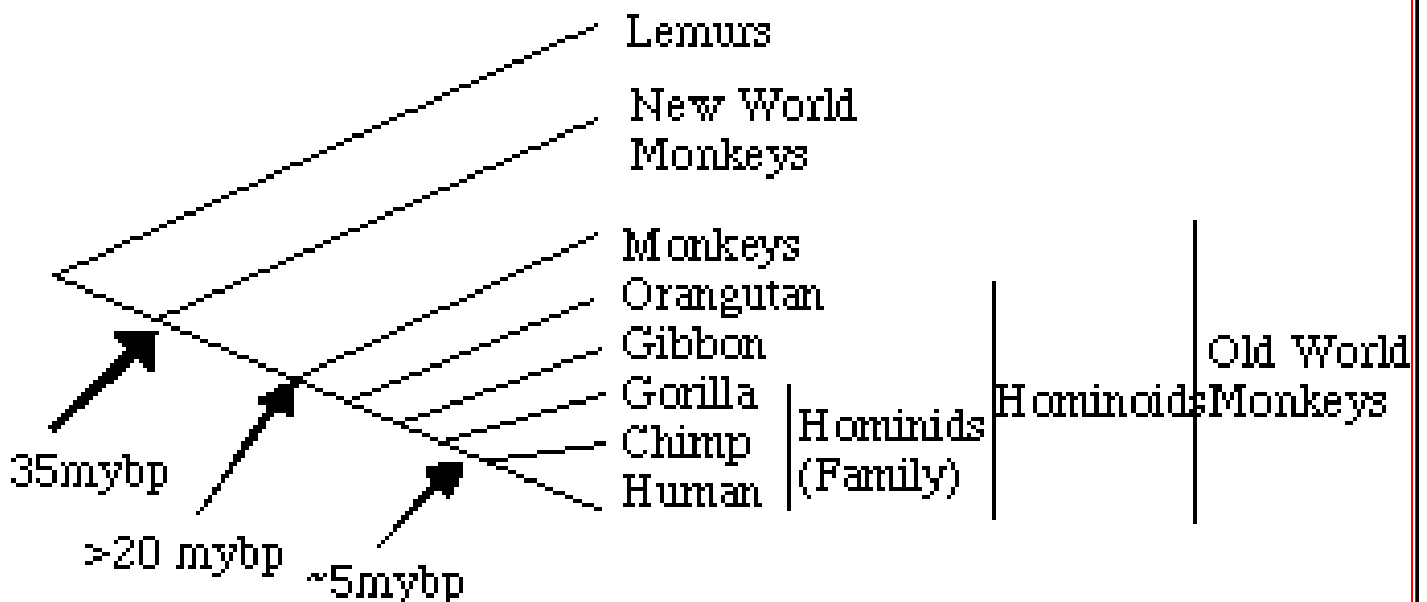
- Species that are extremely similar to one another tend to be clustered geographically (Ex.: Darwin's finches).
- Living species are more similar to fossil species in the same area than they are to living species in other areas

### The law of succession

- General correspondence between fossil and living forms in same geographical area
- Darwin used this observation to predict that fossils of ancient humans should be found in Africa

## 46 Human Evolution

- Humans are too complex to be "understood" by any one field. Thus we will look at a few major steps in evolution and some of the things affecting human evolution.
- Humans are members of the order Primates which consists of about 180 species (there are 17 different orders of mammals which diverged 80-65 million years ago). Primates are a relatively old order of mammals. Most of the synapomorphies of this order are associated with an arboreal way of life: flexible digits, forward facing eyes, vision as a primary sense.
- These traits may have played a role in the evolution of brain size in the lineage leading to humans. Humans are a member of the family Hominidae which is believed to have diverged about 5 million years before the present (mybp) from the other members of the Old world monkeys. At least 20 mybp the Hominoids split off from the other old world monkeys. The dates are rough and get changed now and then.



### Relationship of humans to African apes

Relationship of humans to African apes (chimps, gorillas) and orangutan DNA hybridization indicates that apes are our closest relatives. Human/chimp/gorilla relationships not proven but chimps are most likely our closest relatives. The molecular clock says ~ 5 million years ago the human-chimp line split.

While Chimp and gorilla have knuckle walking, the humans possess many traits associated with bipedality: vertebral column, shape of pelvis, angle of femur, foramen magnum at base of skull. Bipedality seems to be a major "innovation" which allowed humans to enter a new "adaptive zone". The first human (*Australopithecus afarensis*) seems to have an angle between the femur and tibia (Upper and lower leg) that is intermediate to that of humans and gorillas.

### The evolution of modern humans from our hominid ancestor is commonly considered as having involved four major steps:

- evolving terrestriality,
- bipedalism,
- a large brain (encephalization)
- civilization.

There are (and have been) several competing hypotheses that have acknowledged these four steps, but put them in a different sequence during human evolution.

Origin of *Homo sapiens*: *Australopithecus afarensis* = first bipedal hominid, found in east Africa about 3.0-3.2 MYBP. Later forms became more slender (= "gracile"). *Homo habilis* and *H. erectus* (~1.5mybp) came later. The evolution of bipedalism may have freed the hands for us in other functions: carrying, tool use. The trends in the evolution of tool use (more types, more specific tasks, different types of materials, more efficient use of materials) seems to follow (lead??) the evolution of increase cranial capacity. These both seem to increase noticeably about 2 mybp.

### Bipedalism and Brain development

- One theme that involves each of the different sequences of evolution is that there was some feedback that led to the increase in cranial capacity, e.g., becoming bipedal creates selection pressure for a more elaborate brain to control motor function and to process incoming sensory information. This in turn would allow for more successful bipedalism, etc.
- The same argument could be leveled about culture leading to an increase in brain size, and vice versa, so the sequence cannot be resolved just on the logic of feedback loops alone.

### Human Origins

- Origin of "modern humans": Two alternative scenarios for origins:
  - humans originated in more than one site ("Multiregional" model). Evidence supporting this are modern *Homo sapiens* samples found in Asia and Africa

- a single origin ("Noah's Ark" model: one origin and dispersal out from site of origin). Homo sapiens are believed to have originated ~100,000 - 200,000 years ago.
- Paleontological evidence suggests a single origin in Africa. Molecular data shows low genetic diversity worldwide with the highest diversity in Africa, also suggesting an African origin. Recent re-analyses shown that the cladograms of mtDNA cannot support an African origin on statistical grounds.

### Humans, out of Africa

The spread of Homo out of Africa is presumed to have taken place about 1.5 MYBP by Homo erectus. This species seems to be on a trajectory of brain size and body size that looks anagenetic, whereas one lineage that lead to Australopithecus robustus seems to be on another line. In a broad sweep of time, the notion of the chimp leading to the Australopithecine, to Homo, to the Neanderthal to the modern American family standing in their driveway is a myth. There were lineages that diverged in a branching cladogram, some of which did not make it to the present. Evidence for this is provided by more than one distinct morphological type of early humans present at the same time (see below). As time gets closer to modern humans, however (Homo erectus on up), a phyletic gradualist anagenesis is more easy to accept.

### Brain and human evolution

- Once a big brain is achieved and this provides the intellect for an organism to anticipate its environment, the notion that an organism evolves in response to changes of the environment becomes too simplistic..
  - Humans evolved the power to alter their environment so as to protect themselves from its abiotic pressures. This means that they are altering their own selective pressures and a dialectic emerges between the organism and the environment such that these cannot be separated. Other organisms do this (beaver dams, deciduous trees), but in humans this cycle is accelerating

## 47 Proterozoic Eon

### The Length of the Proterozoic

The Proterozoic Eon alone, at 1.955 billion years long, accounts for 42.5% of all geologic time.

### Phanerozoic

Yet the Phanerozoic, consisting of

- Paleozoic,
- Mesozoic,
- Cenozoic eras,

lasted a comparatively brief 545 million years.

### Gunflint Microfossils

Even in well-known Early Proterozoic fossils assemblages, only fossils of bacteria are recognized.

Photomicrograph of spheroidal and filamentous microfossils from the Gunflint Chert of Ontario Canada

### Prokaryote and Eukaryotes

An organism made up of prokaryotic cells is called a prokaryote, whereas those composed of eukaryotic cells are eukaryotes is the basis for the most profound distinction between all living things

### Lack of Organic Diversity

Prokaryotic cells reproduce asexually. Most variation in sexually reproducing populations comes from the shuffling of genes, and their alleles, from generation to generation. Mutations introduce new variation into a population, but their effects are limited in prokaryotes

### Sexual Reproduction Increased the Pace of Evolution

Prior to the appearance of cells capable of sexual reproduction, evolution was a comparatively slow process, thus accounting for the low organic diversity. This situation did not persist. Sexually reproducing cells probably evolved by Early Proterozoic time, and the tempo of evolution increased

### Eukaryotic Cells Evolve

The appearance of eukaryotic cells marks a milestone in evolution comparable to the development of complex metabolic mechanisms such as photosynthesis during the Archean. How do they differ from their predecessors, the prokaryotic cells? All prokaryotes are single-celled, but most eukaryotes are multicelled.

## Eukaryotes

Most eukaryotes reproduce sexually, in marked contrast to prokaryotes, and nearly all are aerobic, that is, they depend on free oxygen to carry out their metabolic processes. Accordingly, they could not have evolved before at least some free oxygen was present in the atmosphere

## Prokaryotic Cell

Prokaryotic Cells are smaller and not nearly as complex as eukaryotic cells

## Eukaryotic Cell

Eukaryotic cells have a cell nucleus containing such as mitochondria and plastids, as well as chloroplasts in plant cells

## Eukaryotic Fossil Cells

The Negaunee Iron Formation in Michigan 2.1 billion years old . Fossils are oldest known eukaryotic cells Bitter Springs Formation of Australia –1 billion yrs old, fossils of single-celled eukaryotes, evidence of meiosis and mitosis, processes carried out only by eukaryotic cells

## Evidence for Eukaryotes

Prokaryotic cells are mostly rather simple spherical or platelike structures. Eukaryotic cells are large much more complex have a well-defined, membrane-bounded cell nucleus, which is lacking in prokaryotes have several internal structures called organelles such as plastids and mitochondria their organizational complexity is much greater than it is for prokaryotes

## Acritarc

These common Late Proterozoic microfossils are probably from eukaryotic organisms. Acritarchs are very likely the cysts of algae

## Late Proterozoic Microfossil

Numerous microfossils of organisms with vase-shaped skeletons have been found in Late Proterozoic rocks, in the Grand Canyon. These too have tentatively been identified as cysts of some kind of algae

## 48 evolutionary biodiversity in Proterozoic Eon

### Evolutionary Biodiversity in Proterozoic Eon

## Endosymbiosis and the Origin of Eukaryotic Cells

Formed from several prokaryotic cells . In a symbiotic relationship Symbiosis involving a prolonged association of two or more dissimilar organisms, is quite common today. In many cases both symbionts benefit from the association as occurs in lichens, once thought to be plants but actually symbiotic fungi and algae

## Evidence for Endosymbiosis

Supporting evidence for endosymbiosis comes from studies of living eukaryotic cells containing internal structures called organelles, such as mitochondria and plastids which contain their own genetic material. In addition, prokaryotic cells synthesize proteins as a single system, whereas eukaryotic cells are a combination of protein-synthesizing systems.

## Organelles Capable of Protein Synthesis

That is, some of the organelles within eukaryotic cells are capable of protein synthesis. These organelles with their own genetic material and protein-synthesizing capabilities are thought to have been free-living bacteria that entered into a symbiotic relationship, eventually giving rise to eukaryotic cells

## Multicelled Organisms

Obviously multicelled organisms are made up of many cells, perhaps billions as opposed to a single cell as in prokaryotes. In addition, multicelled organisms have cells specialized to perform specific functions such as respiration, food gathering and reproduction

## Dawn of Multicelled Organisms

We know from the fossil record that multicelled organisms were present during the Proterozoic but we do not know exactly when they appeared. What seem to be some kind of multicelled algae appear in the 2.1-billion-year-old fossils from the Negaunee Iron Formation in Michigan as carbonaceous filaments from 1.8 billion-year-old rocks in China as somewhat younger carbonaceous impressions of filaments and spherical forms.

## Multicelled Algae?

Carbonaceous impressions in Proterozoic rocks, Montana. These may be impressions of multicelled algae

### The Multicelled Advantage?

Is there any particular advantage to being multicelled? For something on the order of 1.5 billion years all organisms were single-celled and life seems to have thrived. In fact, single-celled organisms are quite good at what they do but what they do is very limited. Single celled organisms can not grow very large, because as size increases proportionately less of a cell is exposed to the external environment in relation to its volume and the proportion of surface area decreases. Transferring materials from the exterior to the interior becomes less efficient. Multicelled organisms live longer, since cells can be replaced and more offspring can be produced. Cells have increased functional efficiency when they are specialized into organs with specific capabilities.

### Other Proterozoic Animal Fossils

- Although scarce, a few animal fossils older than those of the Ediacaran fauna are known.
- A jellyfish-like impression is present in rocks 2000 m below the Ediacara Hills Pound Quartzite.
- Burrows in many areas presumably made by worms, occur in rocks at least 700 million years old.
- Wormlike and algae fossils come from 700 to 900 million-year-old rocks in China but the identity and age of these "fossils" has been questioned

### Soft Bodies

All known Proterozoic animals were soft-bodied, but there is some evidence that the earliest stages in the origin of skeletons was underway. Even some Ediacaran animals may have had a chitinous carapace and others appear to have had areas of calcium carbonate. The odd creature known as *Kimberella* from the latest Proterozoic of Russia had a tough outer covering similar to that of some present-day marine invertebrates.

### Latest Proterozoic *Kimberella*

*Kimberella*, an animal from latest Proterozoic rocks in Russia. Exactly what *Kimberella* was remains uncertain. Some think it was a sluglike creature whereas others think it was more like a mollusk

### Durable Skeletons

Latest Proterozoic fossils of minute scraps of shell-like material and small tooth like denticles and spicules, presumably from sponges indicate that several animals with skeletons or at least partial skeletons existed. More durable skeletons of silica, calcium carbonate, and chitin (a complex organic substance) did not appear in abundance until the beginning of the Phanerozoic Eon 545 million years ago --- Cambrian age

## 49 Evolution of definition of Ecology

### Evolution of Definitions of Ecology

- **Ecology** = from the Greek root OIKOS, "at home", and OLOGY, "the study of" Haeckle (1870):
- "By ecology we mean the body of knowledge concerning the economy of Nature - the investigation of the total relations of the animal to its inorganic and organic environment."
- Burdon-Sanderson (1890s): Elevated Ecology to one of the three natural divisions of Biology: Physiology - Morphology - Ecology
- Elton (1927): "Scientific natural history"
- Andrewartha (1961): "The scientific study of the distribution and abundance of organisms" □
- Odum (1963): "The structure and function of Nature"

### Our Definition

- "Ecology is the scientific study of the processes regulating the distribution and abundance of organisms and the interactions among them, and the study of how these organisms in turn mediate the transport and transformation of energy and matter in the biosphere (i.e., the study of the design of ecosystem structure and function).
- Beyond Fundamental Ecology Applied Ecology: Using ecological principles to maintain conditions necessary for the continuation of present day life on earth.

### Industrial Ecology

The design of the industrial infrastructure such that it consists of a series of interlocking "technological ecosystems" interfacing with global natural ecosystems. Industrial ecology takes the pattern and processes

of natural ecosystems as a design for sustainability. It represents a shift in paradigm from conquering nature to becoming nature.

### Ecological Engineering

Unlike industrial ecology, the focus of Ecological Engineering is on the manipulation of natural ecosystems by humans for our purposes, using small amounts of supplemental energy to control systems in which the main energy drives are still coming from non-human sources. It is the design of new ecosystems for human purposes, using the self-organizing principles of natural ecosystems.

### Ecological Economics

Integrating ecology and economics in such a way that economic and environmental policies are reinforcing rather than mutually destructive.

### Urban ecology

For ecologists, urban ecology is the study of ecology in urban areas, specifically the relationships, interactions, types and numbers of species found in urban habitats. Also, the design of sustainable cities, urban design programs that incorporate political, infrastructure and economic considerations.

### Conservation Biology

The application of diverse fields and disciplines to the conservation of biological diversity. Restoration Biology: Application of ecosystem ecology to the restoration of deteriorated landscapes in an attempt to bring it back to its original state as much as possible. Example, prairie grass.

### Landscape Ecology

"Landscape ecology is concerned with spatial patterns in the landscape and how they develop, with an emphasis on the role of disturbance, including human impacts" (Smith and Smith). It is a relatively new branch of ecology, that employs Global Information Systems. The goal is to predict the responses of different organisms to changes in landscape, to ultimately facilitate ecosystem management

### Organizing principles

All these disciplines require an understanding of the "organizing principles" of ecosystems, i.e., their ecology. This involves the detailed study of the structure and function of ecosystems in their undisturbed state, and using their designs to: determine the resilience of ecosystem functions to human activities. design ecosystems which function in the service of human beings with minimal fossil energy input (ideally none) and minimal waste. design the industrial infrastructure. integrate the value of "goods and services" of natural ecosystems into the global economic system.

### What is "Sustainability"?

There are many definitions of this one, depending on your perspective. Here's ours: Sustainability is a property of a human society in which ecosystems (including humans) are managed such that the conditions supporting present day life on Earth can continue.

## 50 Levels of studying ecology

**Biosphere:** The earth's ecosystem interacting with the physical environment as a whole to maintain a steady state system intermediate in the flow of energy between the high energy input of the sun and the thermal sink of space (merges with atmosphere, lithosphere, hydrosphere...).

**Biome:** Large scale areas of similar vegetation and climatic characteristics.

**Ecosystem:** Set of organisms and abiotic components connected by the exchange of matter and energy (forest, lake, coastal ocean). Or, "the smallest units that can sustain life in isolation from all but atmospheric surroundings."

**Community:** Interacting populations which significantly affect each other's distributions and abundance (intertidal, hot spring, wetland).

**Population:** Group of interacting and interbreeding organisms

- Cell/Organism
- Organelle
- Molecule
- Atom

### Oxidation/reduction reactions

The energy that drives all life processes is organized around oxidation/reduction reactions. Ultimately on Earth today, oxygenic photosynthesis, and energy from the sun, fuels the entire biosphere. Oxygenic photosynthesis produces (by the splitting of water as a reducing agent) one of the most powerful oxidants known – oxygen. The biosphere on the contemporary Earth runs largely on the carbon produced by CO<sub>2</sub> fixation by oxygenic photosynthesis, and on the free energy difference between O<sub>2</sub> and organic carbon, which heterotrophs use to fuel their metabolism.

### Autotrophs

The autotrophs synthesize glucose using solar or chemical energy, which is broken down through respiration (either their own or that of the organisms that eat them) to provide the energy necessary for “biological work”. Redox reactions are central to all of these energy transformations, and the resulting flows of electrons manifest themselves, collectively, in the form of global biogeochemical cycles.

### Role of bacteria

The activities of bacteria keep these cycles moving. For example, the chemosynthetic bacteria oxidize many essential elements in the process of getting the energy required to reduce CO<sub>2</sub>. Certain anaerobic

bacteria in turn reduce these compounds in the process of anaerobic respiration □ i.e., they use them as an electron acceptor in the absence of oxygen. This keeps the element cycles cycling maintaining balanced amounts of oxidants and reductants necessary for diverse metabolic processes. This keeps the system from “running down” energetically. Stay tuned for section on Biogeochemical Cycles.

## 51 Natural history

### Lamarck

Began as a botanist; became the professor responsible for ‘insects, worms and microscopic animals’ at the museum of natural history in Paris. Introduced the vertebrate/invertebrate distinction. Distinguished insects, crustaceans and arachnids. Proposed the first really good system of invertebrates (1801). In that book, he proposed an evolutionary view of life. Proposed ‘biology’ as the title of the science of life.

Interpreted the ladder or chain of being as a real historical series, depicting the evolution of life.

### The chain?

Lamarck realized life couldn’t all be ordered in a single chain; we can only do this within each main group. But evolution works exactly that way for him– it ‘pushes’ living things towards higher and higher positions on the chain. So he needed something other than ‘progressive evolution’ to explain the variety of life– why it seems to have separate branches.

### Branching

The branches arise from adaptation to local conditions. Local conditions alter what the animal does/ how it lives (habits, efforts, activity). This in turn lead it to acquire traits which can be passed on to offspring (when both parents possess them). Nothing new here– but as part of a theory of progressive evolution– that was new.

### Needs

On Lamarck’s account, it’s the animal’s felt needs that produce these changes. So evolution arises from an interaction between organism and environment. This gives us some notion of how adaptation can be explained in a natural way. (Reverses the argument from design: instead of the final causation story, ‘Animals have trait x because x will serve their needs in that environment,’ he says ‘Because x will serve their needs, animals change and acquire x.’ The environment causes the change– no need for design)

### Extinction

For Lamarck, evolution was an alternative to extinction– instead of dying out (in most cases, anyway) ancient animals and plants evolved into different forms that continue today. Lamarck opposed Cuvier’s catastrophism. But Cuvier could cite so many examples of extinction, and Lamarck couldn’t say much about (for instance) which animals today were the descendents of trilobites, etc. Besides, Lamarck’s evolutionary theory was not easy to understand or all that clear: ‘sentiment interieure’ seemed pretty mysterious...

### Cuvier’s advantage

Cuvier’s anatomical and classificational work was impeccable. He identified four basic body plans for animals– vertebrates, molluscs, arthropods, and radiata (jellyfish & others). With these groups clearly distinguished, the chain of being was no longer part of biology. But links between distinct groups were still

striking— Lamarck cited teeth in fetal baleen whales, for instance, which St. Hilaire took as an instance of ‘unity of plan’. A broader sort of unity could restore the chain to some respectability

### **Unity of plan**

St. Hilaire explored the unity of parts and their patterns of development— skeletons in different vertebrates, etc. Established a strong unity of structure for the vertebrates that seemed to go far beyond the demands of Cuvier’s correlation of parts. St. Hilaire tried to expand his unity to animals of different embranchements: vertebrates and mollusks. Cuvier was having none of it— his anatomical knowledge won the day for him again.

### **Von Baer**

Development proceeds up the tree of life. All animals begin as eggs. They develop by multiplying, folding in various ways (patterns preserved throughout large groups of animals) to produce the organs, with details being gradually laid down as development continues. Development thus begins in the same way for each embranchement and only later identifies the particular class, family, genus & species of an organism (in that order).

### **Paleontology**

Meanwhile, Smith, Buckland and Cuvier himself (along with Brongniart) were developing paleontology. The order and regular association of particular species of fossil plants and animals with particular formations was becoming well known. Older species differ substantially from known forms. More familiar forms arise gradually as we examine more recent fossils. The transitions were widely regarded as catastrophic (de Beaumont, for example). But Lyell turned the tide on this, showing that the claims of undeniable catastrophes in the record were much exaggerated.

### **Lyell’s mistake**

As a part of his general resistance to direction/ substantial change in geology, Lyell maintained there was no real direction of change in the fossil record either. This was greeted with pretty general astonishment, but Lyell claimed the apparent changes were just due to our having bad (misleading) samples...more mammals would soon appear in older formations, etc., as we extend our fossil collections. Within ten years (1840) it was clear that this was completely untenable.

### **Gradualism and species**

Since the environment is steadily changing for Lyell, some plants and animals will become extinct because they’re no longer adapted to the environment they’re in (and cannot migrate, for some reason). Where do new species come from? This was a much harder question to answer— though Lyell thought it too would be piecemeal and gradual.

### **But adaptation?**

Aside from Lamarck’s somewhat vague and hard-to-test story of habits, effort and interior sentiment, we have no account here of how living things became adapted to so many different ways of life. Even Lamarck’s account involves effort and needs, so it uses a sort of local final causation to explain how richer, more detailed final causes are worked out. The argument from design remains central here— although it doesn’t explain the tree business (recall the whale’s tooth).

## **52 Life in Water**

Humans everywhere hold a land-centered perspective of the planet. Consequently, aquatic life is often most profuse where conditions appear most hostile to people, for example, along cold, wave-swept seacoasts, in torrential mountain streams, and in the murky waters where rivers meet the sea.

### **The hydrologic cycle exchanges water among reservoirs**

Of the water in the biosphere, the oceans contain 97% and the polar ice caps and glaciers an additional 2%, leaving less than 1% as freshwater. The turnover of water in the various reservoirs of the hydrologic cycle ranges from only 9 days for the atmosphere to 3,100 years for the oceans.

### **Biology of aquatic environments**

The biology of aquatic environments corresponds broadly to variations in physical factors such as light, temperature, and water movements and to chemical factors such as salinity and oxygen.

### **The oceans**

The oceans form the largest continuous environment on earth. An ocean is generally divided vertically into several depth zones, each with a distinctive assemblage of marine organisms. Limited light penetration restricts photosynthetic organisms to the euphotic, or epipelagic, zone and leads to thermal stratification.

Oceanic temperatures are much more stable than terrestrial temperatures. Tropical seas are more stable physically and chemically; temperate and high-latitude seas are more productive. Highest productivity occurs along coastlines. The open ocean supports large numbers of species and is important to global carbon and oxygen budgets.

### **Kelp forests**

Kelp forests are found mainly at temperate latitudes. Coral reefs are limited to the tropics and subtropics to latitudes between 30° N and S latitudes. Coral reefs are generally one of three types: fringing reefs, barrier reefs, and atolls. Kelp beds share several structural features with terrestrial forests. Both seaweeds and reef-building corals grow only in surface waters, where there is sufficient light to support photosynthesis. Kelp forests are generally limited to areas where temperature ranges from about 10° to 20°C, while reef-building corals are limited to areas with temperatures of about 18° to 29°C. The diversity and productivity of coral reefs rival that of tropical rain forests.

### **The intertidal zone**

The intertidal zone lines the coastlines of the world. It can be divided into several vertical zones: the supratidal, high intertidal, middle intertidal, and low intertidal. The magnitude and timing of the tides is determined by the interaction of the gravitational effects of the sun and moon with the configuration of coastlines and basins. Tidal fluctuation produces steep gradients of physical and chemical conditions within the intertidal zone. Exposure to waves, bottom type, height in the intertidal zone, and biological interactions determine the distribution of most organisms within this zone. Salt marshes, mangrove forests, and estuaries occur at the transitions between freshwater and marine environments and between marine and terrestrial environments. Salt marshes, which are dominated by herbaceous vegetation, are found mainly at temperate and high latitudes. Mangrove forests grow in the tropics and subtropics. Estuaries are extremely dynamic physically, chemically, and biologically. The diversity of species is not as high in estuaries, salt marshes, and mangrove forests as in some other aquatic environments but productivity is exceptional.

### **Rivers and streams**

Rivers and streams drain most of the land area of the earth and reflect the land use in their basins. Rivers and streams are very dynamic systems and can be divided into several distinctive environments: longitudinally, laterally, and vertically. The temperature of rivers follows variation in air temperature but does not reach the extremes occurring in terrestrial habitats. The flow and chemical characteristics of rivers change with climatic regime. Current speed, distance from headwaters, and the nature of bottom sediments are principal determinants of the distributions of stream organisms.

### **Lakes**

Lakes are much like small seas. Most are found in regions worked over by tectonics, volcanism

and glacial activity, the geological forces that produce lake basins. A few lakes contain most of the freshwater in the biosphere. Lake structure parallels that of the oceans but on a much smaller scale. The salinity of lakes, which ranges from very dilute waters to over 200‰, is much more variable than that of the oceans. Lake stratification and mixing vary with latitude. Lake flora and fauna largely reflect geographic location and nutrient content

### **Potential threats to aquatic systems**

Potential threats to all these aquatic systems include over-exploitation of populations and waste dumping. Freshwater environments are particularly vulnerable to the introduction of exotic species. The nature of fish assemblages is being used to assess the "biological integrity" of freshwater communities. The application of this Index of Biological Integrity depends on detailed knowledge of the natural history of regional fish faunas

## **53 temperature relations**

### **Microclimates**

Macroclimate interacts with the local landscape to produce microclimates. The sun's uneven heating of the earth's surface and earth's permanent tilt on its axis produce macroclimate. Macroclimate interacts with the local landscape--mainly altitude, aspect, vegetation, color of the ground, and small-scale structural features such as boulders and burrows--to produce microclimates. For the individual organism, macroclimate may be less significant than microclimate. The physical nature of water limits temperature variation in aquatic environments.

### **Temperature Ranges**

Most species perform best in a fairly narrow range of temperatures. The influence of temperature on the performance of organisms begins at the molecular level, where extreme temperatures impair the functioning of enzymes. Rates of photosynthesis and bacterial activity generally peak in a narrow range of temperatures and are much lower outside of this optimal temperature range. How temperature affects the performance of organisms often corresponds to the current distributions of species and their evolutionary histories.

### Regulation of body temperature

Many organisms have evolved ways to compensate for variations in environmental temperature by regulating body temperature. Temperature regulation balances heat gain against heat loss. Plants and ectothermic animals use morphology and behavior to modify rates of heat exchange with the environment. Birds and mammals rely heavily on metabolic energy to regulate body temperature. The physical nature of the aquatic environment reduces the possibilities for temperature regulation by aquatic organisms. Most endothermic aquatic species are air breathers. Some organisms, mainly flying insects and some large marine fish, improve performance by selectively heating parts of their anatomy. The energetic requirements of thermoregulation may influence the geographic distribution of species.

### Survival in extreme temperatures

Many organisms survive extreme temperatures by entering a resting stage. This stage may be as simple as resting in a sheltered spot during the heat of the day or may involve elaborate physiological adjustments. Hummingbirds may enter a state of torpor, a state of low metabolic rate and lowered body temperature, when food is scarce and night temperatures cold. Other animals can go into a state of reduced metabolism that may last several months. If this state occurs mainly in winter, it is called hibernation. If it occurs in summer, it is called estivation. Such reductions in metabolic rate allow these animals to survive extreme environmental conditions during which they must rely entirely on stored energy reserves.

### Effects of habitat destruction and climatic warming

Long-term studies of populations of land snails around Basel, Switzerland, have documented local extinctions of these land snails. These extinctions are attributable to habitat destruction and climatic warming. The results of these studies suggest that climatic warming can lead to the local extinction of species. As we face the prospect of climatic warming at a global scale, studies of temperature relations will assume greater importance.

## 54 Water Relations

### Water Availability

The movement of water down concentration gradients in terrestrial and aquatic environments determines the availability of water to organisms. The most familiar relative measure of the water content of air is relative humidity, defined as water vapor density divided by saturation water vapor density multiplied by 100. On land, the tendency of water to move from organisms to the atmosphere can be approximated by the vapor pressure deficit of the air. Vapor pressure deficit is calculated as the difference between the actual water vapor pressure and the saturation water vapor pressure.

### Movement of water

In the aquatic environment, water moves down its concentration gradient, from solutions of higher water concentration and lower salt content (hypoosmotic) to solutions of lower water concentration and higher salt content (hyperosmotic). This movement of water creates osmotic pressure. Larger osmotic differences, between organism and environment, generate higher osmotic pressures. In the soil-plant system water flows from areas of higher water potential to areas of lower water potential. The water potential of pure water, which by convention is set at zero, is reduced by adding solute and by matric forces, the tendency of water to cling to soil particles and to plant cell walls. Typically, the water potential of plant fluids is determined by a combination of solute concentrations and matric forces, while the water potential of soils is determined mainly by matric forces. In saline soils, solutes may also influence soil water potential. Water potential, osmotic pressure, and vapor pressure deficit can all be measured in pascals (newtons/m<sup>2</sup>), a common currency for considering the water relations of diverse organisms in very different environments.

### Regulation of internal water on terrain

- **Terrestrial plants and animals regulate their internal water by balancing water acquisition against water loss.** Water regulation by terrestrial animals is summarized by

$$W_{ia} = W_d + W_f + W_a - W_e - W_s,$$

where  $W_d$  = drinking,  $W_f$  = taken in with food,  $W_a$  = absorption from the air,  $W_e$  = evaporation and  $W_s$  = secretions and excretions. Water regulation by terrestrial plants is summarized by  $W_{ip} = W_r + W_a - W_t - W_s$ , where  $W_r$  = uptake by roots,  $W_a$  = absorption from the air,  $W_t$  = transpiration, and  $W_s$  = secretions and reproductive structures.

### Survival in arid climates

Some very different terrestrial plants and animals, such as the camel and saguaro cactus, use similar mechanisms to survive in arid climates. Some organisms, such as scorpions and cicadas, use radically different mechanisms. Comparisons such as these suggest that natural selection is opportunistic

### Regulation of internal water in marine environment

Marine and freshwater organisms use complementary mechanisms for water and salt regulation. Marine and freshwater organisms face exactly opposite osmotic challenges. Water regulation in aquatic environments is summarized by:

$$W_i = W_d - W_s + W_o,$$

where **W<sub>d</sub>** = drinking, **W<sub>s</sub>** = secretions and excretions, **W<sub>o</sub>** = osmosis.

### Survival in marine environment

An aquatic organism may either gain or lose water through osmosis, depending on the organism and the environment. Many marine invertebrates reduce their water regulation problems by being isosmotic with seawater. Some freshwater invertebrates also reduce the osmotic gradient between themselves and their environment. Sharks, skates, and rays elevate the urea and TMAO content of their body fluids to the point where they are slightly hyperosmotic to seawater. Marine bony fish and saltwater mosquito larvae are hypoosmotic relative to their environments, while freshwater bony fish and freshwater mosquito larvae are hyperosmotic. While the strength of environmental challenge varies from one environment to another, and the details of water regulation vary from one organism to another, all organisms in all environments expend energy to maintain their internal pool of water and dissolved substances.

### Influence of global-climate change

Scientists who are addressing the question of how global-climate change will influence the distribution of terrestrial vegetation have built a computerized model to predict change in terrestrial biomes across North America. Their model uses what we know about the physiology of major plant growth forms to predict the response of whole biomes. According to the model, climate, the combination of temperature and water availability, determines the distribution of vegetation at large scales, while topography, soils, and fires have local influences. The model gives ecologists a means to explore how various changes in climate may affect the future distributions of biomes.

## 55 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 use  $\text{CO}_2$  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  $\mu\text{mol}$  per square meter per second. Among plants, there are three major alternative photosynthetic pathways,  $\text{C}_3$ ,  $\text{C}_4$ , and CAM.  $\text{C}_4$  and CAM plants are more efficient in their use of water than are  $\text{C}_3$  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 defenses of plants.

### 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 trophically 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 off 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. Energy limitation is a fundamental assumption of optimal foraging theory.

### Optimal foraging theory

**Optimal foraging theory attempts to model how organisms feed as an optimization process.**

Evolutionary ecologists predict that if organisms have limited access to energy, natural selection is likely to favor 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 vexing environmental problems.

## 56 Social Relation

Social relations are important since they often directly and obviously impact the reproductive contribution of individuals to future generations, a key component of evolutionary fitness, the number of offspring, or genes, contributed by an individual to future generations. One of the most fundamental social interactions between individuals takes place during sexual reproduction.

### Mate choice

Mate choice by one sex and/or competition for mates among individuals of the same sex can result in selection for particular traits in individuals, a process called sexual selection. Sexual selection results from differences in reproductive rates among individuals as a result of differences in their mating success. Sexual selection is thought to work either through intrasexual selection, where individuals of one sex compete with each other for mates, or intersexual selection, when members of one sex consistently choose mates from among members of the opposite sex on the basis of some particular trait.

### The case of male guppies

Experimental evidence supports the hypothesis that the coloration of male guppies in local populations is determined by a dynamic interplay between natural selection exerted by predators, under which less colorful males have higher survival, and by female mate choice, which results in higher mating success by more colorful males.

### Scorpionflies

Among scorpionflies, larger males are more likely to successfully defend available arthropod offerings due to their advantages in aggressive encounters and consequently mate more frequently than smaller males without arthropod offerings. Studies of mating in the wild radish, *Raphanus sativus*, in greenhouse and field experiments indicate nonrandom mating and suggest interference competition among pollen from different pollen donors.

### Evolution of sociality

The evolution of sociality is generally accompanied by cooperative feeding, defense of the social group, and restricted reproductive opportunities. The degree of sociality in a social species ranges from acts as simple as mutual grooming or group protection of young to highly complex, stratified societies such as those found in colonies of ants or termites.

## Eusociality

This more complex level of social behavior, which is considered to be the pinnacle of social evolution, is called eusociality. Eusociality is generally thought to include three major characteristics:

- (1) individuals of more than one generation living together,
- (2) cooperative care of young, and
- (3) division of individuals into sterile, or nonreproductive, and reproductive castes.

## Examples

Cooperation among green woodhoopoes and African lions appears to be a response to environmental conditions that require cooperation for success. For green woodhoopoes, the scarcity of high quality territories and intense competition between flocks for those territories create conditions that favor staying in the natal territory and helping raise related young and perhaps inheriting the territory at a later date.

## African lions

To survive, reproduce, and successfully raise offspring to maturity, African lions must work in cooperative groups of females, which are called prides, and of males, which are called coalitions.

## The comparative method for examining eusociality

One of the most valuable tools available to evolutionary biologists is the comparative method. The comparative method examines the characteristics of different species or populations of organisms in a way that attempts to isolate a particular variable or characteristic of interest, such as sociality, while randomizing the influence of confounding, or confusing, variables on the variable of interest. The comparative method has been used to study the evolution of eusociality among a wide variety of animal species including leafcutter ants and naked mole rats, both of which live in social groups in which individuals are divided among castes that engage in very different activities. Compared to other ant species, leafcutter ant colonies have a larger number of castes that engage in a wider variety of behaviors. In contrast to leafcutter ant colonies, where all workers are females, both males and females work in naked mole rat colonies. However, as in leafcutter ant colonies, work in naked mole rat colonies is divided among members according to their size. Many factors have likely contributed to the evolution of eusociality in leafcutter ants and naked mole rats, including kin selection and ecological constraints.

# 57 Population Genetics and Natural Selection

## The rise of modern evolutionary ecology

Darwin and Mendel complemented each other well and their twin visions of the natural world revolutionized biology. The synthesis of the theory of natural selection and genetics gave rise to modern evolutionary ecology. Here we examine four major concepts within the area of population genetics and natural selection.

## Genetic and phenotypic variation

**Populations include genetic and phenotypic variation among individuals, which are significant aspects of population structure.** The first biologists to conduct thorough studies of phenotypic and genotypic variation and to incorporate experiments in their studies, focused on plants. By using plants cloned from the same parent, **Bonnier** was able to control for the effects of genotype on plant form and observe the effects of climate.

## The work of different Scientists

- **Kerner** showed that the differences in growth form observed by him and Bonnier were the result of temporary adjustments to environmental variation and not hereditary changes in the experimental plants.
- **Turesson's** studies provided evidence for genetic differences among populations.
- **Clausen, Keck, and Hiesey** explored the extent and sources of morphological variation in plant populations, including both the influences of environment and genetics.
- **Case** determined that the best predictor of chuckwalla, *Sauromalus*, body length was average winter rainfall.
- **Tracy's** laboratory growth experiments indicated that variation in body size among chuckwalla populations is at least partly determined by genetic differences among populations.

## Hardy-Weinberg equilibrium model

**The Hardy-Weinberg equilibrium model helps identify evolutionary forces that can change gene frequencies in populations.** Because evolution involves changes in gene frequencies in a population, a thorough understanding of evolution must include the area of genetics known as population genetics.

## Hardy-Weinberg principle

One of the most fundamental concepts in population genetics, the Hardy-Weinberg principle, states that “in a population mating at random in the absence of evolutionary forces, allele frequencies will remain constant.”

For a population in Hardy-Weinberg equilibrium in a situation where there are only two alleles at a particular locus,  $p + q = 1.0$ . The frequency of genotypes in a population in Hardy-Weinberg equilibrium can be calculated as  $(p + q)^2 = (p + q) \times (p + q) = p^2 + 2pq + q^2 = 1.0$ .

The conditions necessary to maintain constant allele frequencies in a population are:

- (1) random mating,
- (2) no mutations,
- (3) large population size,
- (4) no immigration, and
- (5) equal survival and reproductive rates for all genotypes.

When a population is not in Hardy-Weinberg equilibrium, the Hardy-Weinberg principle helps us to identify the evolutionary forces that may be in play.

## Genetic drift

Random processes such as genetic drift can change gene frequencies in populations, especially in small populations. Genetic drift is theoretically most effective at changing gene frequencies in small populations such as those that inhabit islands.

## Fragmentation of natural ecosystems

One of the greatest concerns associated with fragmentation of natural ecosystems due to human land use is that reducing habitat availability will decrease the size of animal and plant populations to the point where genetic drift will reduce the genetic diversity within natural populations.

## The work of different Scientists

**Ledig and his colleagues** found a significant positive correlation between population size and genetic diversity in populations of Chihuahua spruce, a naturally fragmented population of trees living on mountain islands.

**Frankham** showed that compared to mainland populations, island populations generally include less genetic variation.

**Saccheri and his colleagues** found that higher heterozygosity (genetic diversity) was associated with lower rates of population extinction through the effects of heterozygosity on larval survival, adult longevity, and egg hatching in populations of the Glanville fritillary butterfly, *Melitaea cinxia*.

## Natural selection

**Natural selection, which changes genetic and phenotypic frequencies in populations, can result in adaptation to the environment.** The most general postulate of the theory of natural selection is that the environment determines the evolution of the anatomy, physiology, and behaviour of organisms. Some of the clearest demonstrations of natural selection have resulted from studies of populations of Galapagos finches. Losos, Warhelt, and Schoener used replicated field experiments to study natural selection for changes in morphology in *Anolis* lizard populations.

## The work of different Scientists

Their results indicate that colonizing populations can adapt rapidly to new environmental conditions.

**Studies by Carroll and several colleagues** show that soapberry bug populations living on native and introduced host plants have undergone natural selection for traits that favor their survival and reproduction on particular host plant species.

## Natural selection

Hundreds of other examples of natural selection have been brought to light during the nearly one and a half century since Darwin published his theory. Still, evolutionary ecology remains a vigorous field of inquiry with plenty of debate, self criticism, and significant work yet to be done.

The earlier research on adaptation of populations to local environmental conditions used transplant experiments to detect genetic differences among populations. More recent research on genetic variation within and among populations has applied techniques developed in molecular biology. Ecologists now have many powerful tools, ranging from classical techniques to modern technologically sophisticated approaches, for assessing the extent of genetic variation within and among populations and meeting the challenge of documenting and conserving biodiversity.

## 58 Population Distribution and Abundance

### Population

Ecologists define a population as a group of individuals of a single species inhabiting an area delimited by natural or human-imposed boundaries. Population studies hold the key to solving practical problems such as saving endangered species, controlling pest populations, or managing fish and game populations. All populations share a number of characteristics including Distribution and abundance.

### Physical environment limits the geographic distribution of species

While there are few environments on earth without life, no single species can tolerate the full range of earth's environments. Because all species find some environments too warm, too cold, too saline, and so forth,

**the physical environment limits the geographic distribution of species.** For instance, there is a close relationship between climate and the distributions of the three largest kangaroos in Australia.

### Examples

The tiger beetle *Cicindela longilabris* is limited to cool boreal and mountain environments. Large- and small-scale variation in temperature and moisture limits the distributions of certain desert plants, such as shrubs in the genus *Encelia*. However, differences in the physical environment only partially explain the distributions of barnacles within the marine intertidal zone, a reminder that biological factors constitute an important part of an organism's environment.

### Distribution patterns of individuals

**On small scales, individuals within populations are distributed in patterns that may be random, regular, or clumped.** Patterns of distribution can be produced by the social interactions within populations, by the structure of the physical environment, or by a combination of the two. Social organisms tend to be clumped; territorial organisms tend to be regularly spaced.

### Clumped distribution

An environment in which resources are patchy also fosters clumped distributions. Aggressive species of stingless bees live in regularly distributed colonies, while the colonies of nonaggressive species are randomly distributed. The distribution of creosote bushes changes as they grow.

**On larger scales, individuals within a population are clumped.** In North America, populations of both wintering and breeding birds are concentrated in a few hot spots of high population density. Clumped distributions are also shown by plant populations living along steep environmental gradients on mountainsides.

### Population density vs increasing organism size

Population density declines with increasing organism size. In general, animal population density declines with increasing body size. This negative relationship holds for animals as varied as terrestrial invertebrates, aquatic invertebrates, birds, poikilothermic vertebrates, and herbivorous mammals. Plant population density also decreases with increasing plant size. However, the biological details underlying the size--density relationship shown by plants are quite different from those underlying the size--density patterns shown by animals. A single species of tree can span a very large range of sizes and densities during its life cycle. The largest trees start life as small seedlings that can live at very high population densities. As trees grow, their population density declines progressively until the mature trees live at low densities.

### Influences on the Rarity

Rarity is influenced by geographic range, habitat tolerance, and population size. Rarity of species can be expressed as a combination of extensive versus restricted geographic range, broad versus narrow habitat tolerance, and large versus small population size. The most abundant species and those least threatened by extinction combine large geographic ranges, wide habitat tolerance, and high local population density. All other combinations of geographic range, habitat tolerance, and population size include one or more attributes of rarity. Rare species are vulnerable to extinction. Populations that combine restricted geographic range with narrow habitat tolerance and small population size are the rarest of the rare and are usually the organisms most vulnerable to extinction.

### Abundance of organisms

The abundance of organisms and how abundance changes in time and space are among the most fundamental concerns of ecology. To estimate the abundance of species the ecologist must contend with a variety of practical challenges and conceptual subtleties. Mark and recapture methods are useful in the study of populations of active, elusive, or secretive animals.

### Mark and recapture techniques

Mark and recapture techniques, which use natural distinguishing marks, are making an important contribution to the study of populations of endangered whales. Ecologists studying organisms, such as corals, algae, and sponges or many types of terrestrial plants that differ a great deal in size and form often estimate abundance as coverage, the area covered by a species. Patterns of distribution and abundance are ultimately determined by underlying population dynamics.

## 59 Population Dynamics

### Survivorship curve

A survivorship curve summarizes the pattern of survival in a population. Patterns of survival can be determined either by following a cohort of individuals of similar age to produce a cohort life table or by determining the age at death of a large number of individuals or the age distribution of a population to produce a static life table.

### Life table

Life tables can be used to draw survivorship curves, which generally fall into one of three categories:

- (1) type I survivorship, in which there is low mortality among the young but high mortality among older individuals;
- (2) type II survivorship, in which there is a fairly constant probability of mortality throughout life; and
- (3) type III survivorship, in which there is high mortality among the young and low mortality among older individuals.

### Age distribution of a population

The age distribution of a population reflects its history of survival, reproduction, and potential for future growth. Age distributions indicate periods of successful reproduction, high and low survival, and whether the older individuals in a population are replacing themselves or if the population is declining.

### Population age structure

Population age structure may be highly complicated in variable environments, such as that of the Galapagos Islands. Populations in highly variable environments may reproduce episodically.

### Net reproductive rate ( $R_0$ )

A life table combined with a fecundity schedule can be used to estimate net reproductive rate ( $R_0$ ), geometric rate of increase ( $\lambda$ ), generation time ( $T$ ), and per capita rate of increase ( $r$ ). Because these population parameters form the core of population dynamics, it is important to understand their derivation as well as their biological meaning.

### Net reproductive rate

Net reproductive rate,  $R_0$ , the average number of off-spring left by an individual in a population, is calculated by multiplying age-specific survivorship rates,  $l_x$ , times age-specific birthrates,  $m_x$ , and summing the results:

$$\sum l_x m_x$$

### Geometric rate of increase

The geometric rate of increase,  $\lambda$ , is calculated as the ratio of population sizes at two successive points in time, Generation time is calculated as:  $T = \sum x l_x m_x / R_0$

### The per capita rate of increase

The per capita rate of increase,  $r$ , is related to generation time and net reproductive rate as:  $r = \ln R_0 / T$

The per capita rate of increase may be positive, zero, or negative depending on whether a population is growing, stable. Or declining.

### Dispersal

Dispersal can increase or decrease local population densities. The contribution of dispersal to

local population density and dynamics is demonstrated by studies of expanding populations of species such as Africanized bees in the Americas and collared doves in Europe.

### Effect of climate change

Climate changes can induce massive changes in the ranges of species. As availability of prey changes, predators may disperse, which increases and decreases their local population densities. Stream organisms actively migrating upstream or drifting downstream increase densities of stationary and migrating populations by immigrating and decrease them by emigrating.

### Effects of pollutants

Ecologists are using the effects of pollutants on population dynamics to predict the potential ecological impact of these pollutants on populations. Good candidates for indicators of pollution are those aspects of population dynamics that are sensitive to environmental variation

### Impact of a wide range of potential pollutants

Based on its environmental sensitivity, per capita rate of increase,  $r$ , appears to be an excellent predictor of the impact of a wide range of potential pollutants. The results of this research suggest that population processes and the mechanisms underlying variation in those processes can be used as sensitive predictors of the ecological effects of environmental change.

## 60 Population Growth

In the presence of abundant resources, populations can grow at geometric or exponential rates. Population growth by organisms with nonoverlapping generations can be described by the geometric model of population growth. Population growth that occurs as a continuous process, as in human or bacterial populations, can be described by the exponential model of population growth.

### Examples of exponential growth

Examples of exponential growth from natural populations suggest that this type of growth may be very important to populations during establishment in new environments, during recovery from some form of exploitation, or during exploitation of transient, favorable conditions.

### Logistic population growth

As resources are depleted, population growth rate slows and eventually stops; this is known as logistic population growth. As population size increases, population growth eventually slows and then ceases, producing a sigmoidal, or S-shaped, population growth curve. Population growth stops when populations reach a maximum size called the carrying capacity, the number of individuals of a particular population that the environment can support.

### Sigmoidal population growth

Sigmoidal population growth can be modelled by the logistic growth equation, a modification of the exponential growth equation that includes a term for environmental resistance. In the logistic model, the rate of population growth decreases as population density increases. Research on laboratory populations indicates that zero population growth at carrying capacity may be attained by many combinations of reduced birthrates and increased death rates.

### Effects of environmental limits

The environment limits population growth by changing birth and death rates. The factors affecting population size and growth include biotic factors such as food, disease, and predators and abiotic factors such as rainfall, floods, and temperature. Because the effects of biotic factors, such as disease and predation, are often influenced by population density, biotic factors are often referred to as density dependent factors. Meanwhile, abiotic factors such as floods and extreme temperature can exert their influences independently of population density and so are often called density-independent factors. As we have already seen, both abiotic and biotic forces have important influences on populations. The significant effects of biotic and abiotic factors on populations have been well demonstrated by studies of Galapagos finches and their major food sources.

### The intrinsic rate of increase( $r_m$ )

On average, small organisms have higher rates of per capita increase,  $r$ , and more variable populations, while large organisms have lower rate of per capita increase and less variable populations. The intrinsic rate of increase,  $r_m$  is the maximum rate of increase for a given species. This rate of increase would occur in the absence of negative environmental influences. The per capita rate of increase,  $r$ , which is the realized rate of increase, is generally less than  $r_m$ . One of the best predictors of  $r_m$  is body size. In general,  $r_m$  decreases with increasing body size, from over 100,000 times from viruses to large vertebrate animals. The present state of the human population can be examined using the conceptual tools of population biology discussed in chapters 9 and 10 and in this chapter. Though humans live on every continent, their population density differs by several orders of magnitude in different regions.

### Global population

In 1997, 61.4% of the global population, or about 3.5 billion people, were concentrated in Asia. The remainder of the human population was spread across Africa (12.8%), Europe (11.8%), North America (7.9%), South America (5.7%), Australia (0.3%), and oceanic islands (0.1%).

### **Sustainable global human population**

Population densities in different regions vary from less than 1 person per square kilometer to nearly 1,000 persons per square kilometer. While the populations of some countries are stable, and some are declining, the global population is expected to continue growing well past the year 2000. One of the greatest environmental challenges of the twenty-first century will be to establish a sustainable global human population.

## **61 Competition**

Competition, interactions between individuals that reduce their fitness, is generally divided into intraspecific competition, competition between individuals of the same species, and interspecific competition, competition between individuals of different species.

### **Forms of Competition**

Competition can take the form of interference competition, direct aggressive interactions, or resource competition in which individuals compete through their dependence on the same limiting resources.

### **Intraspecific competition**

Studies of intraspecific competition provide evidence for resource limitation. Experiments with herbaceous plants show that soil nutrients may limit plant growth rates and plant weight and that competition for nutrients increases with plant population density. Plants reflect their competition for resources, including water, light, and nutrients, through the process of self-thinning. Resource competition among leafhoppers also varies with population density and is reflected in reduced survivorship, smaller size, and increased developmental time at higher population densities. Experiments with terrestrial isopods show that even where there is no food shortage, intraspecific competition through interference may be substantial.

### **Niche**

The niche reflects the environmental requirements of species. The niche concept was developed early in the history of ecology and has had a prominent place in the study of interspecific competition because of the competitive exclusion principle:

### **Same Niche, two species**

Two species with identical niches cannot coexist indefinitely. Hutchinson added the concepts of the fundamental niche, the physical conditions under which a species might live in the absence of other species, and the realized niche, the more restricted conditions under which a species actually lives as the result of interactions with other species. While a species' niche is theoretically defined by a very large number of biotic and abiotic factors, Hutchinson's n-dimensional hypervolume, the most important attributes of the niche of most species, can often be summarized by a few variables. For instance, the niches of Galapagos finches are largely determined by their feeding requirements, while the niche of a salt marsh grass can be defined by tidal levels.

### **Lotka and Volterra**

Mathematical and laboratory models provide a theoretical foundation for studying competitive interactions in nature. Lotka and Volterra independently expanded the logistic model of population growth to represent interspecific competition.

### **Lotka-Volterra competition model**

In the Lotka-Volterra competition model, the growth rate of a species depends both upon numbers of conspecifics and numbers of the competing species. In this model, the effect of one species upon another is summarized by competition coefficients. In general, the Lotka-Volterra competition model predicts coexistence of species when interspecific competition is less intense than intraspecific competition. Competitive exclusion in laboratory experiments suggests the potential for competitive exclusion in nature. Even in the laboratory, however, organisms yield results that are much less predictable than the predictions of the Lotka-Volterra competition equations.

### **Ecological and evolutionary influences on the niches**

Competition can have significant ecological and evolutionary influences on the niches of species. Field experiments involving organisms from herbaceous plants to desert rodents have demonstrated that competition can restrict the niches of species to a narrower set of conditions than they would otherwise occupy in the absence of competition.

### **Natural selection and niches**

Theoretically, natural selection may lead to divergence in the niches of competing species, a situation called character displacement. However, stringent requirements for a definitive demonstration have limited the number of documented cases of character displacement in nature. After many decades of theoretical and

experimental work on competition, we can conclude that competition is a common and strong force operating in nature, but not always and not everywhere.

### Field experiments

The field experiment is one of the most powerful and important tools at the disposal of the field ecologist.

However, the validity of field experiments depends upon several design features, including

1. a testable hypothesis,
2. knowledge of initial conditions,
3. controls, and
4. replication.

## 62 Exploitation

### Predation, Herbivory, Parasitism, and Disease

#### Exploitation

The diversity of interactions between herbivores and plants, between predators and prey, and between parasites, parasitoids, pathogens, and hosts can be grouped under the heading of exploitation--interactions between species that enhance the fitness of one individual at the expense of another.

#### Exploitation weaves populations into a web of relationships that defy easy generalization.

The number of exploitative interactions between species far exceeds the number of species in the biosphere, and the nature of exploitation goes far beyond the typical consumption of one organism by another. For instance, many parasites and pathogens manipulate host behavior to enhance their own fitness at the expense of the host. Spiny-headed worms alter the behavior of a variety of crustacean hosts in a way that increases the probability that the one host species will be eaten by another. A pathogenic fungus manipulates the growth program of its host plant in a way to produce "pseudo flowers," structures aimed at promoting the reproduction of the pathogen. In the process the pathogen usually kills the host plant and always renders it sterile. Predation by one flour beetle species on another can be used as a potent means of interference competition except in the presence of a protozoan parasite, which seems to give a competitive advantage to less predaceous species.

#### Examples

Predators, parasites, and pathogens influence the distribution, abundance, and structure of prey and host populations. Herbivorous stream insects have been shown to control the density of their algal and bacterial food. The herbivorous moth larva *Cactoblastis cactorum* combined with pathogenic microbes reduced the coverage of prickly pear cactus in Australia from millions of hectares to a few thousand. A parasitic infestation reduced the red fox population in Sweden by 70%, which in turn led to increases in the abundance of several prey species eaten by foxes. This parasitic disease revealed the influence of a predator on its prey populations.

#### Relationships

**Predator-prey, parasite-host, and pathogen-host relationships are dynamic.** Populations of a wide variety of predators and prey show highly dynamic fluctuations in abundance ranging from days to decades. A particularly well-studied example of predator-prey cycles is that of snowshoe hares and their predators, which have been shown to result from the combined effects of the snowshoe hares on the quantity and quality of their food and of the predators on the snowshoe hare population.

#### Predator-prey interactions

Mathematical models of predator-prey interactions by Lotka and Volterra suggest that exploitative interactions themselves can produce population cycles without any influences from outside forces such as weather. Predator-prey cycles have also been observed in a few laboratory populations under restricted circumstances.

#### To persist in the face of exploitation, hosts and prey need refuges.

The refuges that promote the persistence of hosts and prey include secure places to which the exploiter has limited access. However, living in large groups can be considered as a kind of refuge since it reduces the probability that an individual host or prey will be attacked. It appears that predator satiation is a defensive tactic used by a wide variety of organisms from rain forest trees to temperate insects. Growing to large size can also represent a kind of refuge when the prey species is faced by size-selective predators. Size is used as a refuge by prey species ranging from stream insects and intertidal invertebrates to rhinoceros.

### Population control

Predators and parasites have been used to control populations of insects that attack crops or to control invasive weeds. Recent research in Kenya has shown that a crayfish, *Procambarus clarkii*, controls the snails that act as intermediate hosts for *Schistosoma*, a highly pathogenic human parasite. Preliminary results indicate that crayfish successfully control host snails in the artificial impoundments used for livestock watering and domestic water, important sources of infection by *Schistosoma*.

## 63 Mutualism

### Mutualism

Mutualism, interactions between individuals that benefit both partners, is a common phenomenon in nature that has apparently made important contributions to the evolutionary history of life and continues to make key contributions to the ecological integrity of the biosphere.

### Mutualisms types

Mutualisms can be divided into those that are facultative, where species can live without their mutualistic partners, and obligate, where species are so dependent on the mutualistic relationship that they cannot live without their mutualistic partners

### Examples

Plants benefit from mutualistic partnerships with a wide variety of bacteria, fungi, and animals. Mutualism provides benefits to plants ranging from nitrogen fixation and enhanced nutrient and water uptake to pollination and seed dispersal.

### Mycorrhiza

Ninety percent of terrestrial plants form mutualistic relationships with mycorrhizal fungi, which make substantial contributions to plant performance. Mycorrhizae, which are mostly either vesicular arbuscular mycorrhizae or ectomycorrhizae, are important in increasing plant access to water, nitrogen, phosphorus, and other nutrients. In return for these nutrients, mycorrhizae receive energy-rich root exudates. Experiments have shown that the mutualistic balance sheet between plants and mycorrhizal fungi can be altered by the availability of nutrients. Plant-ant protection mutualisms are found in both tropical and temperate environments.

### Ants

In tropical environments, many plants provide ants with food and shelter in exchange for protection from a variety of natural enemies. In temperate environments, mutualistic plants provide ants with food but not shelter in trade for protection

### Mutualistic algae

Mutualistic algae called zooxanthellae provide reef-building corals with their principal energy source; in exchange for this energy, corals provide zooxanthellae with nutrients, especially nitrogen, a scarce resource in tropical seas.

### Mutualism between corals

Reef-building corals depend upon mutualistic relationships with algae and animals. The coral-centered mutualisms of tropical seas show striking parallels with terrestrial plant-centered mutualisms. The mutualism between corals and zooxanthellae appears to be largely under the control of the coral partner, which chemically solicits the release of organic compounds from zooxanthellae and controls zooxanthellae population growth. Crabs and shrimp protect some coral species from coral predators in exchange for food and shelter.

### Evolution of Mutualism

Theory predicts that mutualism will evolve where the benefits of mutualism exceed the costs. **Keeler** built a cost-benefit model for the evolution and persistence of facultative plant-ant protection mutualisms in which the benefits of the mutualism to the plant are represented in terms of the proportion of the plant's energy budget that ants protect from damage by herbivores.

The model assesses the costs of the mutualism to the plant in terms of the proportion of the plant's energy budget invested in extrafloral nectaries and the water, carbohydrates, and amino acids contained in the nectar. The model predicts that the mutualism will be favored where there are high densities of ants and potential herbivores and where the effectiveness of alternative defenses are low.

### Humans in Mutualism

Humans have developed a variety of mutualistic relationships with other species, but one of the most spectacular is that between the greater honeyguide and the traditional honey gatherers of Africa. In this apparently ancient mutualism, humans and honeyguides engage in elaborate communication and

cooperation with clear benefit to both partners. The mutualism offers the human side a higher rate of discovery of bees' nests, while the honeyguide gains access to nests that it could not raid without human help. Careful observations have documented that the honeyguide informs the honey gatherers of the direction and distance to bees' nests as well as of their arrival at the nest.

## 64 Specie Abundance and Diversity

### Community

A community is an association of interacting species inhabiting some defined area. Examples of communities include the plant community on a mountainside, the insect community associated with a particular species of tree, or the fish community on a coral reef. Community ecologists often restrict their studies to groups of species that all make their living in a similar way. Animal ecologists call such groups guilds, while plant ecologists use the term life-form. The field of community ecology concerns how the environment influences community structure, including the relative abundance and diversity of species, the subjects of this chapter.

### Abundance

**Most species are moderately abundant; few are very abundant or extremely rare.** Frank Preston (1948) graphed the abundance of species in collections as distributions of species abundance, with each abundance interval twice the preceding one. Preston's graphs were approximately "bell-shaped" curves and are called "lognormal" distributions.

### Lognormal distributions

Lognormal distributions, which describe the relative abundance of organisms ranging from algae and terrestrial plants to birds, may result from many random environmental variables acting upon the populations of a large number of species or may be a consequence of how species subdivide resources. Regardless of the underlying mechanisms, the lognormal distribution is one of the best described patterns in community ecology.

### Species diversity

A combination of the number of species and their relative abundance defines species diversity.

**Two major factors define the diversity of a community:**

- (1) the number of species in the community, which ecologists usually call species richness, and
- (2) the relative abundance of species, or species evenness.

### Shannon-Wiener index

One of the most commonly applied indices of species diversity is the Shannon-Wiener index:

$$H' = - \sum_{i=1}^s p_i \log_e p_i$$

The relative abundance and diversity of species can also be portrayed using rank-abundance curves.

### Species diversity in complex environments

Species diversity is higher in complex environments. Robert MacArthur (1958) discovered that five coexisting warbler species feed in different layers of forest vegetation and that the number of warbler species in North American forests increases with increasing forest stature. Various investigators have found that the diversity of forest birds increases with increased foliage height diversity. The niches of algae can be defined by their nutrient requirements.

### Heterogeneity

Heterogeneity in physical and chemical conditions across aquatic and terrestrial environments can account for a significant portion of the diversity among planktonic algae and terrestrial plants. Soil characteristics and depth to groundwater strongly influence the nature of local plant communities in the Amazon River basin. Increased nutrient availability correlates with reduced algal and plant diversity.

### Disturbance

Intermediate levels of disturbance promote higher diversity. Joseph Connell (1975, 1978) proposed that high diversity is a consequence of continually changing conditions, not of competitive accommodation at equilibrium. He predicted that intermediate levels of disturbance would foster higher levels of diversity. At intermediate levels of disturbance, a wide array of species can colonize open habitats, but there is not enough time for the most effective competitors to exclude the other species.