Pearson New International Edition

Ecology: The Experimental Analysis of Distribution and Abundance

Charles J. Krebs

Sixth Edition

ALWAYS LEARNING

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PEARSON

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Table of Contents

Glossary

abiotic factors characterized by the absence of life; include temperature, humidity, pH, and other physical and chemical influences.

absolute density the number of individuals per unit area or per unit volume.

abundance the number or biomass of organisms of a particular species in a general area.

actual evapotranspiration the actual amount of water that is used by and evaporates from a plant community over a given time period, largely dependent on the available water and the temperature.

adaptation any alteration in the structure or function of an organism by which the organism becomes better able to survive and multiply in its environment.

additive effects reproduction or mortality that simply adds or subtracts the individuals to the current population; opposite of compensatory effects.

aggregation coming together of organisms into a group, as in locusts.

aggregative response the response of predators or parasitoids to concentrate their foraging in an area of dense prey species.

Allee effects population growth rates that decrease below replacement level at low population density, potentially leading to extinction.

allele one of a pair of characters that are alternative to each other in inheritance, being governed by genes situated at the same locus in homologous chromosomes.

allelopathy organisms that alter the surrounding chemical environment in such a way as to prevent other species from using it, typically with toxins or antibiotics.

ambient energy hypothesis the idea that species diversity is governed by the amount of energy falling on an area.

apex predator in a food chain, it is the highest trophic level. Apex predators do not have other predators feeding on them within the food web.

aposematic warning coloration, indicating to a predator that this prey is poisonous or highly defended against attack.

apparent competition two species who do not share any resources but whose numbers change in relation to one another because of an indirect effect of a third species, typically a shared predator or natural enemy.

association major unit in community ecology, characterized by essential uniformity of species composition.

autotroph organism that obtains energy from the sun and materials from inorganic sources; contrast with *heterotroph*. Most plants are autotrophs.

balance of nature the belief that natural populations and communities exist in a stable equilibrium and maintain that equilibrium in the absence of human interference.

barriers any geographic feature that hinders or prevents dispersal or movement across it, producing isolation.

basal metabolic rate the amount of energy expended by an animal while at rest in a neutral temperate environment, in the post-absorptive (fasting) state; the minimum rate of metabolism.

big-bang reproduction offspring are produced in one burst rather than in a repeated manner.

biodiversity the number of species in a community or region, which may be weighted by their relative abundances; also used as an umbrella concept for total biological diversity including genetic diversity within a species, species diversity (as used here), and ecosystem diversity at the community or ecosystem level of organization.

bioelements the chemical elements that move through living organisms.

biogeochemical cycles the movement of chemical elements around an ecosystem via physical and biological processes.

biogeography the study of the geographical distribution of life on Earth and the reasons for the patterns one observes on different continents, islands, or oceans.

biological control the reduction of pests by the introduction of predators, parasites, or pathogens; by genetic manipulations of crops or pests; by sterilization of pests; or by mating disruption using pheromones.

biomanipulation the management practice of using a trophic cascade to restore lakes to a clear water condition by removing herbivorous or planktivorous fishes or by adding piscivorous (predatory) fishes to a lake.

biomass the mass or weight of living matter in an area.

biosphere the whole-earth ecosystem, also called the *ecosphere.*

biota species of all the plants and animals occurring within a certain area or region.

biotic factors environmental influences caused by plants or animals; opposite of abiotic factors.

bottom-up model the idea that community organization is set by the effects of plants on herbivores and herbivores on carnivores in the food chain.

bryophytes plants in the phylum Bryophyta comprising mosses, liverworts, and hornworts.

Calvin-Benson cycle the series of biochemical reactions that takes place in the stroma of chloroplasts in photosynthetic organisms and

From *Ecology*: *The Experimental Analysis of Distribution and Abundance*, Sixth Edition. Eugene Hecht.

results in the first step of carbon fixation in photosynthesis.

cannibalism an animal that feeds on others of the same species.

carnivores animals that eat mainly flesh from other animals; contrast with *herbivore*.

catastrophic agents term used by Howard and Fiske (1911) to describe agents of destruction in which the percentage of destruction is not related to population density; synonymous with density-independent factors.

character displacement the divergence in morphology between similar species in the region where the species both occur, but this divergence is reduced or lost in regions where the species' distributions do not overlap; presumed to be caused by competition.

climatic climax the final equilibrium vegetation for a site that is dictated by climate and toward which all successions are proceeding, according to Frederic Clements.

climax community the final equilibrium community toward which succession moves.

climax-pattern hypothesis the view that climax communities grade into one another and form a continuum of climax types that vary gradually along environmental gradients.

closed population in population estimation, a population that is not changing in size during the interval of study, having no natality, mortality, immigration, or emigration.

coarse-grained habitat from a particular species' point of view a habitat is coarse grained if it spends its life in one fragment of habitat and cannot move easily to another patch.

coevolution the evolution of two or more species that interact closely with one another, with each species adapting to changes in the other.

cohort life table a life table that follows a group of organisms from germination, birth, or hatching to the death of the last individual.

common garden an experimental design in plant ecophysiology in which a series of plants from different areas are brought together and planted in one area, side by side, in an attempt to determine which features of the plants are genetically controlled and which are environmentally determined.

community a group of populations living in the same area or habitat.

community structure the species composition of an ecological community including the abundance of all the populations in the community.

compartment any component of study for an analysis of nutrient cycling, such as a lake, a species of plant, or a functional group of nitrogen fixers, measured by its standing crop or amount of nutrient.

compartment model a type of box-and-arrow model of diseases in which each compartment contains a part of the system that can be measured and the compartments are linked by flows between them; each compartment typically has an input from some compartments and an output to other compartments.

compensation point for plants the equilibrium point at which photosynthesis equals respiration.

compensatory effects reproduction or mortality that does not add or subtract the individuals to the current population but only replaces other individuals with no change in population size; opposite of additive effects.

competition occurs when a number of organisms of the same or different species utilize common resources that are in short supply (*exploitation*) or when the organisms harm one another in the process of acquiring these resources (*interference*).

competitive exclusion principle complete competitors cannot coexist; also called Gause's hypothesis.

connectance used to describe food web complexity; the fraction of potential interactions in a food web that actually exist.

continental climates the product of weather systems over large landmasses that result in cold winters and warm summers, not influenced by the large ocean masses, typically in temperate and polar latitudes.

control in an experimental design a control is a treatment or plot in which nothing is changed so that it serves as a baseline for comparison with the experimental treatments to which something is typically added or subtracted.

cost–benefit analysis an assessment to determine whether the cost of an activity is less than the benefit that can be expected from the activity.

crassulacean acid metabolism (CAM) a form of photosynthesis in which the two chemical parts of photosynthesis are separated in time because CO_2 is taken up at night through the stomata (which are then closed during the day) and fixed to be used later in the day to complete photosynthesis carbon fixation; an adaptation used by desert plants to conserve water.

critical load the amount of a nutrient such as nitrogen that can be absorbed by an ecosystem without damaging its integrity.

cultural control the reduction of pest populations by agricultural manipulations involving crop rotation, strip cropping, burning of crop residues, staggered plantings, and other agricultural practices.

declining-population paradigm the focus of this approach is on detecting, diagnosing, and halting a population decline by finding the causal factors affecting the population.

deme interbreeding group in a population; also known as *local population*.

demographic stochasticity the random variation in birth and death rates that can lead by chance to extinction.

demographic transition the change in human populations from the two zero-population-growth states of high birth and high death rates to low birth and low death rates.

density number of organisms per unit area or per unit volume.

density-dependent rate as population density rises, births or immigration decrease or deaths or emigration increase, and consequently a graph of population density versus the rate will have a positive or negative slope.

density-independent rate as population density rises, the rate does not change in any systematic manner, so that a graph of population

density versus the rate will have a slope of zero.
determinate layers birds that lay a fixed number of eggs no matter what occurs.
deterministic extinctions losses of species due to the removal of an essential resource.
deterministic models mathematical models with a fixed outcome, models that give the same answer every time they are repeatedly run with a fixed set of parameters; opposite of *stochastic model*.
detritus the plant production not consumed by herbivores.
developmental response the increasing intake rate of prey items by an organism that is growing in size as it develops.
dilution rate general term to describe the rate of additions to a population from birth and immigration.
directional selection natural selection that favors traits either above or below the average of the population, so that over time the average moves in one direction.
disease a pathological condition of an organism resulting from various causes, such as an infection, a genetic disorder, or environmental stress, with specific symptoms.
dispersal the movement of individuals away from their place of birth or hatching or seed production into a new habitat or area to survive and reproduce.
disruptive selection natural selection that favors extreme trait values rather than intermediate values so that over time extreme traits become more common.
disturbance any short-lived strong disruption to an ecological population or community, such as a fire, flood, windstorm, or earthquake.
dominant species common species of large biomass or numbers in a community.
dynamic pool models a model to predict maximum sustained yield based on detailed population information on growth rates, natural mortality, and fishing mortality; contrast with *logistic-type model*.
dynamic stability hypothesis for food chain length suggests that higher trophic levels are less stable than lower trophic levels and past a certain point the longer chains go extinct.
dynamics in population ecology, the study of the reasons for changes in population size; contrast with *statics*.
ecological footprint the total land and water area that is appropriated by a nation or a city to produce all the resources it consumes and to absorb all the waste it generates.
ecological longevity average length of life of individuals of a population under stated conditions.
ecological specialization model a proposed explanation for Hanski's Rule, which postulates that species that exploit a wide range of resources become both widespread and common; these species are generalists; also called Brown's model.
ecosystem biotic community and its abiotic environment; the whole Earth can be considered as one large ecosystem.
ecosystem services all the processes through which natural ecosystems and the biodiversity they contain help sustain human life on Earth.
ecotone transition zone between two diverse communities (e.g., the tundra–boreal forest ecotone).
ecotype a genetic subspecies or race of a plant or animal species that is adapted to a specific set of environmental conditions such as temperature or salinity.
edaphic pertaining to the soil.
effective population size a population genetic concept of the number of breeding individuals in an idealized population that would maintain the existing genetic variability; it is typically much less than the observed population size.
Eltonian pyramid abundance or biomass of successive trophic levels of an ecosystem, illustrating the impact of energy flows through successive trophic transfers.
emigration the movement of individuals out of an area occupied by the population, typically the site of birth or hatching.
endemic phase for locusts and other organisms that show outbreaks, the phase of low numbers when individuals are difficult to find in the field.
endemic species species that occur in one restricted area but in no other.
energetic hypothesis for food chain length, postulates that higher trophic levels are restricted by the limited efficiency of energy transfer along the chain.
environment all the biotic and abiotic factors that actually affect an individual organism at any point in its life cycle.
environmental heterogeneity variation in space in any environmental parameter such as soil pH or tree cover.
environmental stochasticity variation in population growth rates imposed by changes in weather and biotic factors, as well as natural catastrophes such as floods and hurricanes.
epidemic phase for locusts and other species that show rapid increases to high density, the phase of high numbers and maximum damage; contrast with *endemic phase*.
epidemiology branch of medicine dealing with epidemic diseases.
epipelic algae algae living in or on the sediments of a body of water.
equilibrium model of community organization the global view that ecological communities are relatively constant in composition and are resilient to disturbances.
equitability evenness of distribution of species abundance patterns; maximum equitability occurs when all species are represented by the same number of individuals.
eutrophic lake a highly productive lake with dense phytoplankton, typically with green water.
eutrophic soils soils with high nutrient levels, mostly recent and often volcanic in origin.
eutrophication the process by which lakes are changed from clear water lakes dominated by green algae into murky lakes dominated by blue-green algae, typically caused by nutrient runoffs from cities or agriculture.
evapotranspiration sum total of water lost from the land by evaporation and plant transpiration.

experiment test of a hypothesis. It can be observational (observe the system) or manipulative (perturb the system). The experimental method is the scientific method.

experimental analysis an approach to studying population regulation that relies on the manipulation of populations rather than simple observation of changes used in key factor analysis.

facilitation helping another organism, providing positive feedback in a population interaction.

facilitation model the classic view that succession proceeds via one species helping the next species in the sequence to establish.

fact particular truth of the natural world. Philosophers endlessly discuss what a fact is. Ecologists make observations, which may be faulty; consequently, every observation is not automatically a fact.

facultative agents term used by Howard and Fiske (1911) to describe agents of destruction that increase their percentage of destruction as population density rises; synonymous with *density-dependent factors*.

fecundity an organism's potential reproductive capacity over a period of time, measured by the number of gametes produced.

feeding guilds organisms that eat the same general foods, such as seed-eaters.

fertility the actual number of viable offspring produced by an organism over a period of time, equivalent to realized *fecundity*.

fertility schedule the age-specific reproductive output per individual.

field metabolic rate the amount of energy used per unit of time by an organism under normal conditions of life in a natural ecosystem.

fine-grained habitat from a particular species' point of view, a habitat is fine grained if it moves freely from one patch to another at no cost.

First Principle of Population Regulation no closed population stops increasing unless either the per capita birth rate or death rate is density dependent.

fitness the ability of a particular genotype or phenotype to leave descendants in future generations, relative to other organisms.

flux rate the rate of flow of nutrients or biomass from one compartment to another.

food chain the transfer of energy and materials from plants to herbivores to carnivores.

food web a linked set of *food chains* that most often resemble a web.

frost drought for plants a shortage of water in winter when the ground is frozen so no water can be taken up by the roots and yet air temperature is high enough that plants attempt to photosynthesize.

functional group a group of species that perform the same function in a community.

functional response the change in the intake rate of a predator in relation to the density of its prey species.

fundamental niche the ecological space occupied by a species in the absence of competition and other biotic interactions from other species.

Gause's hypothesis complete competitors cannot coexist; also called the competitive exclusion principle.

gene flow the movement of alleles of genes in space and time from one population to another.

genecology study of population genetics in relation to the habitat conditions; the study of species and other taxa by the combined methods and concepts of ecology and genetics.

generalist predators predators that eat a great variety of prey species.

generalists species that eat a variety of foods or live in a variety of habitats; contrast to *specialists*.

genet a unit of genetically identical individuals, derived by asexual reproduction from a single original zygote.

genetic stochasticity any potential loss of genetic variation due to inbreeding or genetic drift (the nonrandom assortment of genes during reproduction).

genotype entire genetic constitution of an organism; contrast with *phenotype*.

genotypic under the control of the genetic endowment of an individual.

global nutrient cycles nutrient cycles that operate at very large scales over much of the Earth because the nutrients are volatile, such as oxygen.

global stability occurs when a community can recover from any disturbance, large or small, and go back to its initial configuration of species composition and abundances; compare with *neighborhood stability*.

gradocoen totality of all factors that impinge on a population, including *biotic* agents and *abiotic* factors.

grazing facilitation the process of one herbivore creating attractive feeding conditions for another herbivore so there is a benefit provided to the second herbivore.

green world hypothesis the proposed explanation for the simple observation that the world is green, that herbivores are held in check by their predators, parasites, and diseases, although other explanations have been suggested.

greenhouse effect the process in which the emission of infrared (long-wave) radiation by the atmosphere warms a planet's surface.

greenhouse gases gases present in the Earth's atmosphere that reflect infrared radiation back to Earth, thus warming it. The most important ones affected by humans are carbon dioxide, methane, nitrous oxide, and chlorofluorocarbons. Water vapor also acts as a greenhouse gas.

gross primary production the energy or carbon fixed via photosynthesis per unit time.

gross production production before respiration losses are subtracted; photosynthetic production for plants and metabolizable production for animals.

gross productivity the assimilation rate of an animal, which includes all the digested energy less the urinary waste.

group selection natural selection for traits that favor groups within a species irrespective of whether the traits favor individuals or not.

growth form morphological categories of plants, such as trees, shrubs, and vines.

guild a group of species that exploit a common resource base in a similar fashion.

habitat a particular environment in which a species lives, or broadly speaking the biotic environment occupied by an individual or population.
habitat selection the behavioral actions of organisms (typically animals) in choosing the areas in which they live and breed.
handling time the time utilized by a predator to consume an individual prey item.
Hanski's Rule the generalization that there is a positive relationship between distribution and abundance, such that abundant species have wide geographical ranges.
harvest method the measurement of primary production by clipping the vegetation at two successive times.
herbivore an animal that eats plants or parts of plants; contrast with *carnivore*.
herbivory the eating of parts of plants by animals, not typically resulting in plant death.
heterogeneity the distribution of relative abundance among the species.
heterotroph organism that obtains energy and materials by eating other organisms; contrast with *autotroph*.
homeostasis maintenance of constancy or a high degree of uniformity in an organism's functions or interactions of individuals in a population or community under changing conditions; results from the capabilities of organisms to make adjustments.
homeothermic pertaining to warm-blooded animals that regulate their body temperature; contrast with *poikilothermic*.
host organism that furnishes food, shelter, or other benefits to another organism of a different species.
hotspots of biodiversity areas of the Earth that contain many endemic species (typically 1500) and as such are of important conservation value.
hydrophyte plant that grows wholly or partly immersed in water; compare with *xerophyte* and *mesophyte*.
hypothesis universal proposition that suggests an explanation for some observed ecological situation.
hypoxia lack of oxygen, typically in lakes or parts of an ocean basin in which excessive primary production is broken down by bacteria and other decomposers, using up all the oxygen in the water.
ideal despotic distribution a theoretical spatial spread of members of a population in which the competitive dominant "aggressive" individuals take up the best resources or territories, and less competitive individuals take up areas or resources in direct relationship to their dominance status.
ideal free distribution a theoretical spatial spread of members of a population in which individuals take up areas with equal amounts of resources in relation to their needs, so all individuals do equally well (the polar opposite to the ideal despotic distribution).
immigration the movement of organisms into an area.
immunocontraception the use of genetic engineering to insert genes that stimulate the immune system of a vertebrate to reject sperm or eggs, thus causing infertility.
incidence functions the fraction of patches of a given size occupied by a breeding population of a particular species.
indeterminate layers birds that continue to lay eggs until the nest is full, thus compensating for any egg removals.
index of similarity ratio of the number of species found in common in two communities to the total number of species that are present in both.
indifferent species species occurring in many different communities; are poor species for community classification.
individual optimization hypothesis that each individual in a population has its own optimal clutch size, so that not all individuals are identical.
inducible defenses plant defense methods that are called into action once herbivore attack occurs and are nearly absent during periods of no herbivory.
inhibition model succession proceeds via one species trying to stop the next species in the sequence from establishing.
initial floristic composition the model of succession of who-gets-there-first wins, part of the inhibition model.
insect parasitoids insects that lay their eggs in or on the host species, so that the larvae enter the host and kill it by consuming it from the inside.
integrated pest management (IPM) the use of all techniques of control in an optimal mix to minimize pesticide use and maximize natural controls of pest numbers.
interactive herbivore system plant-herbivore interactions in which there is feedback from the herbivores to the plants so that herbivores affect plant production and fitness.
intermediate disturbance hypothesis the idea that biodiversity will be maximal in habitats that are subject to disturbances at a moderate level, rather than at a low or high level.
interspecific between two or more different species.
interspecific competition competition between members of different species.
intransitive competition a competitive network that never reaches a fixed endpoint because A replaces B and B replaces C but C can replace A.
intraspecific between individuals of the same species.
intrinsic capacity for increase (r) measure of the rate of increase of a population under controlled conditions, with fixed birth and death rates; also called *innate capacity for increase*.
irruption a rapid increase in a population, often after being introduced to a new area, followed by a collapse that may be rapid or prolonged and may result in a convergent oscillation to a lower equilibrium density.
isocline a contour line in graphical presentations of mathematical models in which some parameter is equal all along the line.
isotherm line drawn on a map or chart connecting points with the same temperature at a particular time or over a certain period.
key factor analysis a systematic approach using life tables to determine the factors responsible for the regulation and fluctuation of populations.
keystone species relatively rare species in a community whose removal causes a large shift in the structure

of the community and the extinction of some species.

kin selection the evolution of traits that increase the survival, and ultimately the reproductive success, of one's relatives.

Krantz anatomy the particular type of leaf anatomy that characterizes C_4 plants; plant veins are encased by thick-walled photosynthetic bundle-sheath cells that are surrounded by thin-walled mesophyll cells.

***K*-selection** the type of natural selection experienced by organisms that live at carrying capacity or maximal density in a relatively stable environment.

Lack clutch size the clutch size at which productivity is maximal for the population.

Lack's hypothesis that clutch size in birds is determined by the number of young that parents can provide with food.

Leslie matrix model a method of casting the age-specific reproductive schedule and the age-specific mortality schedule of a population in matrix form so that predictions of future population change can be made.

Liebig's law of the minimum the generalization first stated by Justus von Liebig that the rate of any biological process is limited by that factor in least amount relative to requirements, so there is a single limiting factor.

life table the age-specific mortality schedule of a population.

limiting factor a factor is defined as limiting if a change in the factor produces a change in average or equilibrium density.

littoral shallow-water zone of lakes or the sea, with light penetration to the bottom; often occupied by rooted aquatic plants.

local nutrient cycles nutrient cycles that are confined to small regions because the elements are non-volatile, such as the phosphorus cycle.

local population see *deme*.

local population model a proposed explanation for Hanski's Rule, which assumes that species differ in their capacity to disperse, and if the environment is divided into patches, some species will occupy more local patches than others as a function of their dispersal powers.

local stability occurs when communities recover from only small disturbances and return to their former configuration of species composition and abundances.

logistic equation model of population growth described by a symmetrical S-shaped curve with an upper asymptote.

logistic-type model type of optimum-yield model in which the yield is predicted from an overall descriptive function of population growth without a separate analysis of the components of mortality, recruitment, and growth; contrast with *dynamic pool model*.

log-normal distribution the statistical distribution that has the shape of a normal, bell-shaped curve when the *x*-axis is expressed in a logarithmic scale rather than an arithmetic scale.

loss rate general term to describe the rate of removal of organisms from a population by death and emigration.

Lotka-Volterra equations the set of equations that describe competition between organisms for food or space; another set of equations describes predator-prey interactions

lottery competition a type of interference competition in which an individual's chances of winning or losing are determined by who gets access to the resource first.

macroparasites large multicellular organisms, typically arthropods or helminths, which do not multiply within their definitive hosts but instead produce transmission stages (eggs and larvae) that pass into the external environment.

marine protected area a national park in the ocean where fishing is restricted or eliminated for the purpose of protecting populations from overharvesting.

match-mismatch hypothesis the idea that population regulation in many fish is determined in the early juvenile stages by food supplies, so that if eggs hatch at the same time that food is abundant, many will survive, but if eggs hatch when food is scarce, many will die.

matrix models a family of models of population change based on matrix algebra, with the Leslie matrix model being the best known.

maximum economic rent the desired economic goal of any exploited resource, measured by total revenues – total costs.

maximum reproduction the theory that natural selection will maximize reproductive rate, subject to the constraints imposed by feeding and predator avoidance.

maximum sustained yield (MSY) the predicted yield that can be taken from a population without the resource collapsing in the short or long term.

mean length of a generation the average length of time between the birth of a female and her offspring.

mechanism a biological process that explains some phenomenon.

mesic moderately moist.

mesophyte plant that grows in environmental conditions that include moderate moisture conditions.

mesopredators secondary consumers (e.g., carnivores) in a food chain that are fed upon by tertiary consumers such as apex predators.

metabolic theory of ecology an attempt to derive patterns of individual performance, population, and ecosystem dynamics from the fundamental observation that the metabolic rate of individuals is related to body size and temperature.

metapopulations local *populations* in patches that are linked together by dispersal among the patches, driven by colonization and extinction dynamics.

microparasites small pathogenic organisms, typically protozoa, fungi, bacteria, or viruses, that can cause disease.

minimum viable population (MVP) the size of a population in terms of breeding individuals that will ensure at some specified level of risk continued existence with ecological and genetic integrity.

model verbal or mathematical statement of a hypothesis.

modular organisms organisms that have an indefinite growth form, such as plants or corals.

monoclimax hypothesis the classic view of Frederic Clements that all vegetation in a region converges ultimately to a single climax plant community.

monogamy mating of an animal with only one member of the opposite sex.

morphology study of the form, structure, and development of organisms.

mortality the death of organisms in a population.

multivoltine refers to an organism that has several generations during a single season; contrast with *univoltine*.

mutualism a relationship between two organisms of different species that benefits both and harms neither.

mycorrhizae a mutually beneficial association of a fungus and the roots of a plant in which the plant's mineral absorption is enhanced and the fungus obtains nutrients from the plant.

natality birth or germination or hatching; reproductive output of a population.

natural control the limitation of pest populations by predators, parasitoids, parasites, diseases, and weather in the absence of chemical control.

natural selection the process in nature by which only the organisms best adapted to their environment tend to survive and transmit their genetic characteristics to succeeding generations while those less adapted tend to be eliminated.

neighborhood stability also called *local stability,* the ability of a community to return to its former configuration after a small disturbance.

nested subsets a sequence of habitat patches, ordered by size, is nested if all the species in the smaller patches are also included in the larger patches.

net primary production the energy (or carbon) fixed in photosynthesis minus the energy (or carbon) lost via respiration per unit time.

net production production after respiration losses are subtracted.

net reproductive rate (R_0) the average number of offspring produced per female or reproductive unit.

niche the ecological space occupied by a species, and the occupation of the species in a community.

niche breadth a measurement of the range of resources utilized by a species.

niche overlap a measure of how much species overlap with one another in the use of resources.

nonequilibrium model of community organization the global view that ecological communities are not constant in their composition because they are always recovering from *biotic* and *abiotic* disturbances, never reaching an equilibrium.

noninteractive herbivore system plant-herbivore interactions in which there is no feedback from the herbivores to the plants.

numerical response the change in the numbers or density of a predator in relation to changes in the density of its prey species.

obligate predator or parasite that is restricted to eating a single species of prey.

oligochaetes any of a class or order (Oligochaeta) of hermaphroditic terrestrial or aquatic annelids lacking a specialized head; includes earthworms.

oligotrophic lake an unproductive, clear-water lake with a low density of phytoplankton.

oligotrophic pattern soils of very low nutrient levels that are common in tropical areas and regions with geologically old, highly eroded soils with most of the nutrients in the litter layer.

omnivore an animal that feeds on both plants and animals in a food chain.

open population in population estimation, a population that has natality, mortality, immigration, or emigration during the interval of study.

optimal defense hypothesis the idea that plants allocate defenses against herbivores in a manner that maximizes individual plant fitness, and that defenses are costly to produce.

optimal foraging any method of searching for and obtaining food that maximizes the relative benefit.

optimal foraging theory a detailed model of how animals should forage to maximize their fitness.

optimal group size the size that results in the largest relative benefit.

optimality models models that assume natural selection will achieve adaptations that are the best possible for each trait in terms of survival and reproduction.

optimum yield amount of material that can be removed from a population to maximize biomass (or numbers, or profit, or any other type of "optimum") on a sustained basis.

ordination process by which plant or animal communities are ordered along a gradient.

overcompensation hypothesis the idea that a small amount of grazing will increase plant growth and fitness rather than cause harm to the plant.

paradox of the plankton the problem of understanding how many phytoplankton species that have the same basic requirements can coexist in a community without competitive exclusion.

parasite an organism that grows, feeds, or is sheltered on or in a different organism while harming its host.

parasitoid an insect that completes larval development in another insect host.

parthenogenesis development of the egg of an organism into an embryo without fertilization.

patch any discrete area, regardless of size.

pesticide any chemical that kills a plant or animal pest.

pesticide suppression the reduction of pest populations with herbicides, fungicides, insecticides, or other chemical poisons.

Petersen method a population estimation procedure based on two periods of mark-and-recapture.

phenology study of the periodic (seasonal) phenomena of animal and plant life and their relations to the weather and climate (e.g., the time of flowering in plants).

phenotype expression of the characteristics of an organism as determined by the interaction of its genic constitution and the environment; contrast with *genotype*.

photoperiodism the physiological responses of plants and animals to the length of day.

photosynthesis the series of chemical reactions in plants that results in the fixation of carbon from CO_2 into some form of carbohydrate.

photosynthetically active radiation (PAR) that part of the solar radiation spectrum in the range 0.4 to 0.7 μm that can be used for photosynthesis by green leaves.

physiological ecology the subdiscipline of ecology that studies the biochemical, physical, and mechanical adaptations and limitations of plants and animals to their physical and chemical environments.

physiological longevity maximum life span of individuals in a population under specified conditions; the organisms die of senescence.

phytoplankton plant portion of the plankton; the plant community in marine and freshwater environments that floats free in the water and contains many species of algae and diatoms.

Plant Apparency Theory the hypothesis that herbivores attack plants that are highly visible and common, and the more apparent a plant is to herbivores, the more it must invest in defensive chemicals and structures.

plant stress hypothesis the idea that herbivores prefer to attack stressed plants, which produce leaves that are higher in nitrogen.

plant vigor hypothesis the idea that herbivores prefer to attack fast-growing, vigorous plants rather than slow-growing, stressed plants.

poikilothermic of or pertaining to cold-blooded animals, organisms that have no rapidly operating heat-regulatory mechanism; contrast with *homeothermic*.

polyandry mating of a single female animal with several males.

polyclimax hypothesis the view of Whittaker that there are several different climax vegetation communities in a region governed by many environmental factors.

polygyny mating of one male animal with several females.

pool the amount of nutrient or biomass in a compartment.

population a group of organisms of the same species occupying a particular space at a particular time.

population regulation the general problem of what prevents populations from growing without limit, and what determines the average abundance of a species.

potential evapotranspiration the theoretical depth of water that would evaporate from a standard flat pan over a given time period if water is not limiting, largely dependent on temperature.

precipitation rainfall and snowfall over a specified time period.

predation the action of one organism killing and eating another.

preemptive initial floristics model the first species at a site take over and prevent others from colonizing the site, emphasizing inhibition as the main mechanism of succession.

prey isocline the contour line of densities of predator and prey at which the prey are in equilibrium; the impact of a predator exactly balances the prey's rate of population growth, so the prey population growth rate is zero.

primary production production by green plants.

primary succession succession occurring on a landscape that has no biological legacy.

principle universal statement that we all accept because they are mostly definitions, or are ecological translations of physical–chemical laws. For example, "no population increases without limit" is an important ecological principle that must be correct in view of the finite size of the planet Earth.

probabilistic models in contrast to deterministic models, including an element of probability so that repeated runs of the models do not produce exactly the same outcome.

production amount of energy (or material) formed by an individual, population, or community in a specific time period; includes growth and reproduction only; see *primary production*, *secondary production*, *gross production*, *net production*.

productivity a general term that covers all processes involved in ecological *production* studies—carbon fixation, consumption, rejection, leakage, and respiration.

promiscuity a general term for multiple matings in organisms, called polyandry if multiple males are involved, or polygyny if multiple females; opposite of *monogamy.*

proximate factors the mechanisms responsible for regulating a particular trait in a physiological or biochemical manner; opposite of *ultimate factors*.

push-pull strategies management strategies that manipulate the behavior of insect pests to make the crop resource unattractive (push) and lure the pests toward an attractive source (pull) where the pests are destroyed.

quadrat a sampling frame for stationary organisms; a square, circle, or rectangle of a specified size.

ramet an individual derived by asexual reproduction from a single original zygote, which is able to live independently if separated from the parent organism. Compare with *genet*.

random colonization model succession proceeds completely randomly with no fixed sequence or fixed end point.

Rapoport's Rule the generalization that geographic range sizes decrease as one moves from polar to equatorial latitudes, such that range sizes are smaller in the tropics.

realized niche the observed resource use of a species in the presence of competition and other biotic interactions; contrast with *fundamental niche*.

reciprocal replacement two codominant plants retain their presence in the climax community by A replacing B while B replaces A.

recruitment increment to a natural population, usually from young animals or plants entering the adult population.

Red Queen Hypothesis the coevolution of parasites and their hosts, or predators and their prey, in which improvements in one of the species is countered by evolutionary improvements in the partner species, so that an evolutionary arms race occurs but neither species gains an advantage in the interaction.

Redfield ratio the observed 16:1 atomic ratio of nitrogen to phosphorus found in organisms in the open ocean by A. C. Redfield in 1934—$C_{106}N_{16}P_1$.

regulating factor a factor is defined as potentially regulating if the percentage of mortality caused by the factor increases with population density or if per capita reproductive rate decreases with population density.

Reid's paradox the observed large discrepancy between the rapid rate of movement of trees recolonizing areas at the end of the Ice Age and the observed slow dispersal rate of tree seeds spreading by diffusion.

relative benefit the difference between the costs and benefits (= net benefit).

relative density the density of a population in relation to another, specified in terms of larger/smaller without knowing the absolute density.

relay floristics the classical view of succession as specified in the facilitation model.

repeated reproduction organisms that reproduce several times over their life span.

replacement series an experimental design involving two or more species in competition in which a series of ratios are set out (such as 20:80 or 50:50) and some measure of performance is measured.

reproductive value the contribution an individual female will make to the future population.

residence time the time a nutrient spends in a given compartment of an ecosystem; equivalent to turnover time.

resilience magnitude of disturbance that can be absorbed before an ecosystem changes its structure; one aspect of ecosystem stability.

Resource Availability Hypothesis a theory of plant defense that predicts higher plant growth rates will result in less investment in defensive chemicals and structures.

resource concentration hypothesis the idea that agricultural pests are able to cause serious damage because crops are planted as monocultures at high densities.

respiration complex series of chemical reactions in all organisms by which energy is made available for use; carbon dioxide, water, and energy are the end products.

***r*-selection** the type of natural selection experienced by populations that are undergoing rapid population increase in a relatively empty environment.

safe sites for animals, sites where prey individuals are able to avoid predation; for plants, sites where seeds can germinate and plants can grow.

sampling model one proposed explanation for Hanski's Rule that the observed relationship between distribution and abundance is an artifact of the difficulty of sampling rare species and does not therefore require a biological explanation.

saprophyte plant that obtains food from dead or decaying organic matter.

scientific law universal statement that is deterministic and so well corroborated that everyone accepts it as part of the scientific background of knowledge. There are laws in physics, chemistry, and genetics, but not yet in ecology.

Second Principle of Population Regulation differences between two populations in equilibrium density can be caused by variation in either density-dependent or density-independent per capita birth and death rates.

secondary plant substances chemicals produced by plants that are not directly involved in the primary metabolic pathways and whose main function is to repel herbivores.

secondary production production by herbivores, carnivores, or detritus feeders; contrast with *primary production*.

secondary succession succession occurring on a landscape that has a biological legacy in the form of seeds, roots, and some live plants.

self-regulation process of population regulation in which population increase is prevented by a deterioration in the quality of individuals that make up the population; population regulation by adjustments in behavior and physiology within the population rather than by external forces such as predators.

self-thinning rule the prediction that the regression of organism size versus population density has a slope of –1.5 for plants and animals that have plastic growth rates and variable adult size.

senescence process of aging.

seral referring to a series of stages that follow one another in an ecological succession.

serotinous cones cones of some pine trees that remain on the trees for several years without opening and require a fire to open and release the seeds.

sessile attached to an object or fixed in place (e.g., barnacles).

shade-intolerant plants plants that cannot survive and grow in the shade of another plant, requiring open habitats for survival.

shade-tolerant plants plants that can live and grow in the shade of other plants.

Shelford's law of tolerance the ecological rule first described by Victor Shelford that the geographical distribution of a species will be controlled by that environmental factor for which the organism has the narrowest range of tolerance.

sigmoid curve S-shaped curve; in ecology, often a plot of time (x-axis) against population size (y-axis); an example is the logistic curve.

sink populations local populations in which the rate of production is below replacement level so that extinction is inevitable without a source of immigrants.

small-population paradigm the focus of this approach is on rare species and on the population consequences of rareness, and the abilities of small populations to deal with rarity.

soil drought the lack of water in the soil, less than what is needed for plant survival and growth, caused by a lack of precipitation.

source populations local populations in which the rate of production exceeds replacement so that individuals emigrate to surrounding populations.

specialist predators predators that eat only one or a very few prey species.

specialists species that eat only a few foods or live in only one or two habitats; contrast to *generalists*.

species richness the number of species in a community.

species-area curve a plot of the area of an island or habitat on the x-axis and the number of species in that island or habitat on the

y-axis, typically done as a log-log plot and typically restricted to one taxonomic group such as plants or reptiles.

stability absence of fluctuations in populations; ability to withstand perturbations without large changes in composition.

stabilizing selection natural selection that favors the norm, the most common or average trait in a population, so the population mean stays constant.

stable age distribution the age distribution reached by a population growing at a constant rate.

stable point an equilibrium in a mathematical model to which the system converges and remains.

stage-based matrix model a type of matrix model not based on organism ages but on life history stages, such as larva, pupa, and adult.

standard error a statistical estimate of the precision of an estimate such as the mean.

static life table a life table constructed at a single point in time by doing a cross section of a population.

statics in population ecology, the study of the reasons of equilibrium conditions or average values; contrast with *dynamics*.

stationary age distribution the age distribution that is reached in a population that is constant in size over time because the birth rate equals the death rate.

steppe extensive area of natural, dry grassland; usually used in reference to grasslands in southwestern Asia and southeastern Europe; equivalent to prairie in North American usage.

sterile-insect technique the release of large numbers of sterilized males to mate with wild females and prevent the fertilization of eggs and production of viable young.

sterol any of a group of solid, mostly unsaturated polycyclic alcohols, such as cholesterol or ergosterol, derived from plants and animals.

stochastic based on probability, as in coin-flipping.

stochastic model mathematical model based on probabilities; the prediction of the model is not a single fixed number but a range of possible numbers; opposite of *deterministic model*.

stock the harvestable part of the population being exploited.

stock-recruit relationship a key graph relating how many recruits come into the exploited population from a given population of adults.

stress a condition occurring in response to adverse external influences and capable of affecting the performance of an organism, for example, in plants in a drought.

sublethal effects any pathogenic effects that reduce the well-being of an individual without causing death.

sublittoral lower division in the sea from a depth of 40 to 60 meters to about 200 meters; below the littoral zone.

succession replacement of one kind of community by another kind; the progressive changes in vegetation and animal life that may culminate in the *climax state*.

supply-side ecology the view that population dynamics are driven by immigration of seeds or juveniles from sources extrinsic to the local population, so there is no local control of recruitment processes.

sustainability the characteristic of a process that can be maintained at a certain level indefinitely, often used in an economic and environmental context. Many definitions have been suggested. The original one of the Bruntland Commission of 1987 defined sustainable development as development that meets the needs of the present without compromising the ability of future generations to meet their own needs.

symbiosis in a broad sense, the living together of two or more organisms of different species; in a narrow sense, synonymous with *mutualism*.

synecology study of groups of organisms in relation to their environment; includes population, community, and ecosystem ecology.

taiga the northern boreal forest zone, a broad band of coniferous forest south of the arctic tundra.

tannins a class of secondary compounds produced by plants (and present in tea and coffee) that reduce the digestibility of plant tissues eaten by herbivores; tannins have been used for centuries to tan animal hides.

tens rule the rule of thumb that 1 species in 10 alien species imported into a country becomes introduced, 1 in 10 of the introduced species becomes established, and 1 in 10 of the established species becomes a pest.

territory any defended area.

theory an integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of scientific observations. The theory of evolution is perhaps the most frequently used theory in ecology.

thermoregulation maintenance or regulation of temperature, specifically the maintenance of a particular temperature of the living body.

theta-logistic model the modification of the original logistic equation to permit curved relationships between population density and the rate of population increase.

tillers ramets, the modular unit of construction, for example, in grasses.

time lags in population models, basing a parameter on past events, such as basing population growth rate on the density of the population last year or the year before.

tolerance model the view that plants in a successional sequence do not interact with one another in either a negative or a positive manner.

top-down model the idea that community organization is set by the effects of carnivores on herbivores and herbivores on plants in the food chain.

total fertility rate number of children a woman could expect to produce in her lifetime if the birth rate were held constant at current conditions.

total response the total losses imposed on a prey species by a combination of the numerical, functional, aggregative, and developmental responses of a predator species.

trace element chemical element used by organisms in minute quantities and essential to their physiology.

trade-offs compromises between two desirable but incompatible activities.

tragedy of the commons the inherent tendency for overexploitation of resources that have free access and unlimited demand, so that it pays the individual to continue harvesting beyond the limits dictated by the common good of sustainability.

transitive competition a linear competitive network in which A wins over B and B wins over C, so that the results of competition reach a final state of competitive exclusion.

treeline the altitude on a mountain above which no trees can survive, equivalent of timberline.

trophic cascade model the idea that a strict top-down model applies to community organization so that impacts flow down the food chain as a series of + and – impacts on successive trophic levels.

trophic efficiency net production at one trophic level as a fraction of net production of the next lower trophic level.

trophic levels classification of organisms based on their source of energy—i.e., primary producers, herbivores, carnivores, and higher carnivores.

tundra treeless area in arctic and alpine regions, varying from a bare area to various types of vegetation consisting of grasses, sedges, forbs, dwarf shrubs, lichens, and mosses.

ultimate factors the evolutionary reason for an adaptation or why a trait is maintained in a population; opposite of *proximate factors*.

umbrella species in conservation biology, species that serve as a proxy for entire communities and ecosystems, so that the entire system is conserved if they are conserved.

unitary organisms organisms appear as individual units with a definite growth form, like most animals.

univoltine refers to an organism that has only one generation per year.

unstable point an equilibrium in a mathematical model from which the system diverges and does not remain.

vector organism organism (often an insect) that transmits a pathogenic virus, bacterium, protozoan, or fungus from one organism to another.

virulence the degree or ability of a pathogenic organism to cause disease; often measured by the host death rate.

wilting point measure of soil water; the water remaining in the soil (expressed as percentage of dry weight of the soil) when the plants are in a state of permanent wilting from water shortage.

xeric deficient in available moisture for the support of life (e.g., desert environments).

xerophyte plant that can grow in dry places (e.g., cactus).

yield amount of usable material taken from a harvested population, measured in numbers or biomass.

zooplankton animal portion of the plankton; the animal community in marine and freshwater environments that floats free in the water, independent of the shore and the bottom, moving passively with the currents.

Introduction to the Science of Ecology

Key Concepts

- Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms.
- Descriptive ecology forms the essential foundation for functional ecology, which asks *how* systems work, and for evolutionary ecology, which asks *why* natural selection has favored this particular solution.
- Ecological problems can be analyzed using a theoretical approach, a laboratory approach, or a field approach.
- Like other scientists, ecologists observe problems, make hypotheses, and test the predictions of each hypothesis by field or laboratory observations.
- Ecological systems are complex, and simple cause–effect relationships are rare.

From Chapter 1 of *Ecology: The Experimental Analysis of Distribution and Abundance,* Sixth Edition. Eugene Hecht.

KEY TERMS

experiment Test of a hypothesis. It can be observational (observe the system) or manipulative (perturb the system). The experimental method is the scientific method.

hypothesis Universal proposition that suggests explanations for some observed ecological situation. Ecology abounds with hypotheses.

model Verbal or mathematical statement of a hypothesis.

principle Universal statement that we all accept because they are mostly definitions, or are ecological translations of physical–chemical laws.

scientific law Universal statement that is deterministic and so well corroborated that everyone accepts it as part of the scientific background of knowledge. There are laws in physics, chemistry, and genetics, but not yet in ecology.

theory An integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of scientific observations. The theory of evolution is perhaps the most frequently used theory in ecology.

Introduction to the Science of Ecology

You are embarking on a study of ecology, the most integrative discipline in the biological sciences. The purpose of this chapter is to get you started by defining the subject, providing a small amount of background history, and introducing the broad concepts that will serve as a road map for the details to come.

Definition of Ecology

The word *ecology* came into use in the second half of the nineteenth century. Ernst Haeckel in 1869 defined ecology as the total relations of the animal to both its organic and its inorganic environment. This very broad definition has provoked some authors to point out that if this is ecology, there is very little that is *not* ecology. Four biological disciplines are closely related to ecology—genetics, evolution, physiology, and behavior (**Figure 1**). Broadly interpreted, ecology overlaps each of these four subjects; hence, we need a more restrictive definition.

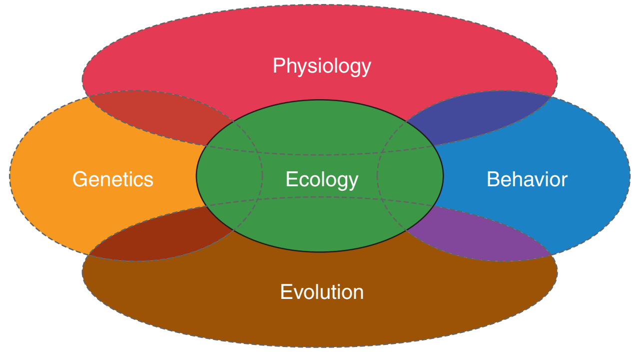

Figure 1 The four biological disciplines closely related to ecology.

Charles Elton in his pioneering book *Animal Ecology* (1927) defined ecology as scientific natural history. Although this definition points out the origin of many of our ecological problems, it is again uncomfortably vague. In 1963 Eugene Odum defined ecology as the study of the structure and function of nature. This statement emphasizes the form-and-function idea that permeates biology, but it is still not a completely clear definition. A clear but restrictive definition of ecology is this: Ecology is the scientific study of the distribution and abundance of organisms (Andrewartha 1961). This definition is static and leaves out the important idea of relationships. Because ecology is about relationships, we can modify Andrewartha's definition to make a precise definition of **ecology**: *Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms*.

This definition of ecology appropriately constrains the scope of our quest, and is the meaning that will be adopted in this chapter. To better understand what ecology is, we need to know what is special about scientific studies, and what is meant by distribution and abundance. **Distribution**—where organisms are found—and **abundance**—how many organisms are found in a given area—are key facts that must be determined before we can address the most difficult question: *Why* this particular distribution, *why* this abundance? We seek the cause-and-effect relationships that govern distribution and abundance.

History of Ecology

The historical roots of ecology are varied, and in this section we will explore briefly some of the origins of ecological ideas. We are not the first humans to think about ecological problems. The roots of ecology lie in natural history. Primitive tribes, for example—who depended on hunting, fishing, and food gathering—needed detailed knowledge of where and when their quarry might be found. The establishment of agriculture also increased the need to learn about the ecology of plants and domestic animals. Agriculture today is a special form of applied ecology.

Outbreaks of pests such as locusts in the Middle East and North Africa or rats in rice crops in Asia are not new problems in agriculture. Spectacular plagues of animals attracted the attention of the earliest writers. The Egyptians and Babylonians feared locust plagues (**Figure 2**), often attributing them to supernatural powers (Exodus 7:14–12:30). In the fourth century B.C., Aristotle tried to explain plagues of field mice and locusts in *Historia Animalium*. He pointed out that the high reproductive rate of field mice could produce more mice than could be reduced by their natural predators, such as foxes and ferrets, or by the control efforts of humans. Nothing succeeded in reducing these mouse plagues, Aristotle stated, except the rain, and after heavy rains the mice disappeared rapidly. And even today, Australian wheat farmers face plagues of house mice, and ask the same question: How can we get rid of these pests?

Pests are a problem for people because they violate our feeling of harmony or balance in the environment. Ecological harmony was a guiding principle basic to the Greeks' understanding of nature. The historian Frank Egerton (1968a) has traced this concept from ancient times to the modern term *balance of nature*. The concept of *providential ecology*, in which nature is designed to benefit and preserve each species, was implicit in the writings of Herodotus and Plato. A major assumption of this concept was that the number of every species remained essentially constant. Outbreaks of some populations were acknowledged, but were usually attributed to divine punishment. And since each species had a special place in nature, extinction could not occur because it would disrupt the balance and harmony in nature.

Figure 2 A young girl looks at a dense swarm of the desert locust in North Africa.

How did we get from these early Greek and Roman ideas about harmony to our modern understanding? A combination of mathematics and natural history paved the way. By the seventeenth century students of natural history and human ecology began to focus on population ecology and to construct a quantitative framework. Graunt, who in 1662 described human population change in quantitative terms, can be called the "father of demography"[1] (Cole 1958). He recognized the importance of measuring birth rates, death rates, and age structure of human populations, and he complained about the inadequate census data available in England in the seventeenth century. Graunt estimated the potential rate of population growth for London, and concluded that even without immigration, London's population would double in 64 years.

Today, human population growth is an increasing concern, but population growth was not always measured quantitatively for animals and plants. Leeuwenhoek made one of the first attempts to calculate theoretical rates of increase for an animal species (Egerton 1968b). He studied the reproductive rate of grain beetles, carrion flies, and human lice, counting the number of eggs laid by female carrion flies and calculating that one pair of flies could produce 746,496 flies in three months.

By the eighteenth century, natural history had become an important cultural occupation. Buffon, who authored *Natural History* (1756), touched on many of our modern ecological problems and recognized that populations of humans, other animals, and plants are subjected to the same processes. Buffon discussed, for example, how the great fertility of every species was counterbalanced by innumerable agents of destruction. He believed that plague populations of field mice were checked partly by diseases and scarcity of food. Buffon did not accept Aristotle's idea that heavy rains caused the decline of dense mouse populations, but thought instead that control was achieved by biological agents. Rabbits, he stated, would reduce the countryside to a desert if it were not for their predators. If the Australians had listened to Buffon before they introduced rabbits to their environment in 1859, they could have saved their rangelands from destruction (**Figure 3**). Buffon in 1756 was dealing with problems of population regulation that are still unsolved today.

Malthus, the most famous of the early demographers, published one of the earliest controversial books on demography, *Essay on Population* (1798). He calculated that although the number of organisms can increase geometrically (1, 2, 4, 8, 16,. . .), food supply can

[1]Demography originated as the study of human population growth and decline. It is now used as a more general term that includes plant and animal population changes.

Figure 3 European rabbit overpopulation in eastern Australia. Rabbits were introduced to Australia in 1859 and have become a serious pest because of their abundance. Their burrowing increased soil erosion, and they competed with sheep and cattle for forage.

never increase faster than arithmetically (1, 2, 3, 4,. . .). The arithmetic rate of increase in food production seems to be somewhat arbitrary. The great disproportion between these two powers of increase led Malthus to infer that reproduction must eventually be checked by food production. What prevents populations from reaching the point at which they deplete their food supply? What checks operate against the tendency toward a geometric rate of increase? Two centuries later we still ask these questions. These ideas were not new; Machiavelli had said much the same thing around 1525, as did Buffon in 1751, and several others had anticipated Malthus. It was Malthus, however, who brought these ideas to general attention. Darwin used the reasoning of Malthus as one of the bases for his theory of natural selection. The struggle for existence results from the high reproductive output of species.

Other workers questioned the ideas of Malthus and made different predictions for human populations. For example, in 1841 Doubleday put forward the True Law of Population. He believed that whenever a species was threatened, nature made a corresponding effort to preserve it by increasing the fertility of its members. Human populations that were undernourished had the highest fertility; those that were well fed had the lowest fertility. You can make the same observations by looking around the world today (**Table 1**). Doubleday explained these effects by the oversupply of mineral nutrients in well-fed populations. Doubleday observed a basic fact that we recognize today: low birth rates occur in wealthy countries—although his explanations were completely wrong.

Interest in the mathematical aspects of demography increased after Malthus. Can we describe a mathematical law of population growth? Quetelet, a Belgian statistician, suggested in 1835 that the growth of a population was checked by factors opposing population growth. In 1838 his student Pierre-François Verhulst derived an equation describing the initial rapid growth and eventual leveling off of a population over time. This S-shaped curve he called the logistic curve. His work

Table 1 Total fertility rate of human populations and gross national income per person in selected countries of the globe in 2007.

Country	Total fertility rate	Gross national income per person
Sudan	4.5	2160
Gambia	5.1	1970
Niger	7.1	830
Tanzania	5.4	740
Botswana	3.1	12,240
South Africa	2.7	11,710
Canada	1.5	34,610
United States	2.1	44,260
Costa Rica	1.9	10,770
Mexico	2.4	11,330
Haiti	4.0	1490
Brazil	2.3	8800
Peru	2.5	6070
Turkey	2.2	9060
India	2.9	3800
Pakistan	4.1	2500
Indonesia	2.4	3950
China	1.6	7730
Japan	1.3	33,730
Sweden	1.9	34,780
Switzerland	1.4	40,630
Russia	1.3	11,620
Italy	1.4	29,840
Solomon Islands	4.5	2170

The total fertility rate is the average number of children a woman would have, assuming no change in birth rates. The gross national income (GNI) is in U.S. dollars per person. (Data from 2007 World Population Data Sheet.)

was overlooked until modern times, but it is fundamentally important, and we will return to it later in detail.

Until the nineteenth century, philosophical thinking had not changed from the idea of Plato's day that there was harmony in nature. Providential design was still the guiding light. In the late eighteenth and early nineteenth centuries, two ideas that undermined the idea of the balance of nature gradually gained support: (1) that many species had become extinct and (2) that resources are limited and competition caused by population pressure is important in nature. The consequences of these two ideas became clear with the work of Malthus, Lyell, Spencer, and Darwin in the nineteenth century. Providential ecology and the balance of nature were replaced by natural selection and the struggle for existence (Egerton 1968c).

The balance of nature idea, redefined after Darwin, has continued to persist in modern ecology (Pimm 1991). The idea that natural systems are stable and in equilibrium with their environments unless humans disturb them is still accepted by many ecologists and theoreticians.

Humans must eat, and many of the early developments in ecology came from the applied fields of agriculture and fisheries. Insect pests of crops have been one focus of work. Before the advent of modern chemistry, biological control was the only feasible approach. In 1762 the mynah bird was introduced from India to the island of Mauritius to control the red locust; by 1770 the locust threat was a negligible problem (Moutia and Mamet 1946). Forskål wrote in 1775 about the introduction of predatory ants from nearby mountains into date-palm orchards to control other species of ants feeding on the palms in southwestern Arabia. In subsequent years, an increasing knowledge of insect parasitism and predation led to many such introductions all over the world in the hope of controlling nonnative and native agricultural pests (De Bach 1974).

Medical work on infectious diseases such as malaria in the late 1800s gave rise to the study of epidemiology and interest in the spread of disease through a population. Malaria is still one of the great scourges of humans. In 1900 no one even knew the cause of the disease. Once mosquitoes were pinpointed as the vectors, medical workers realized that it was necessary to know in detail the ecology of mosquitoes. The pioneering work of Robert Ross (1911) attempted to describe in mathematical terms the propagation of malaria, which is transmitted by mosquitoes. In an infected area, the propagation of malaria is determined by two continuous and simultaneous processes: (1) The number of new infections among people depends on the number and infectivity of mosquitoes, and (2) the infectivity of mosquitoes depends on the number of people in the locality and the frequency of malaria among them. Ross could write these two processes as two simultaneous differential equations:

$$\begin{pmatrix}\text{Rate of increase of}\\ \text{infected humans}\end{pmatrix} = \underset{\substack{\downarrow \\ \text{(Depends on number of infected mosquitoes)}}}{\begin{pmatrix}\text{New infections}\\ \text{per unit time}\end{pmatrix}} - \begin{pmatrix}\text{Recoveries per}\\ \text{unit time}\end{pmatrix}$$

$$\begin{pmatrix}\text{Rate of increase of}\\ \text{infected mosquitoes}\end{pmatrix} = \underset{\substack{\downarrow \\ \text{(Depends on number of infected humans)}}}{\begin{pmatrix}\text{New infections}\\ \text{per unit time}\end{pmatrix}} - \begin{pmatrix}\text{Death of infected}\\ \text{per unit time}\end{pmatrix}$$

Ross had described an ecological process with a mathematical model, and his work represents a pioneering parasite–host model of species interactions. Such models can help us to clarify the problem—we can analyze the components of the model—and predict the spread of malaria or other diseases.

Production ecology, the study of the harvestable yields of plants and animals, had its beginnings in agriculture, and Egerton (1969) traced this back to the eighteenth-century botanist Richard Bradley. Bradley recognized the fundamental similarities of animal and plant production, and he proposed methods of maximizing agricultural yields (and hence profits) for wine grapes, trees, poultry, rabbits, and fish. The conceptual framework that Bradley used—monetary investment versus profit—is now called the "optimum-yield problem" and is a central issue in applied ecology.

Individual species do not exist in a vacuum, but instead in a matrix of other species with which they interact. Recognition of communities of living organisms in nature is very old, but specific recognition of the interrelations of the organisms in a community is relatively recent. Edward Forbes in 1844 described the distribution of animals in British coastal waters and part of the Mediterranean Sea, and he wrote of zones of differing depths that were distinguished by the associations of species they contained. Forbes noted that some species are found only in one zone, and that other species have a maximum of development in one zone but occur sparsely in other adjacent zones. Mingled in are stragglers that do not fit the zonation pattern. Forbes recognized the dynamic aspect of the interrelations between these organisms and their environment. As the environment changed, one species might die out, and another might increase in abundance. Karl Möbius expressed similar ideas in 1877 in a classic essay on the oyster-bed community as a unified collection of species.

Studies of communities were greatly influenced by the Danish botanist J. E. B. Warming (1895, 1909), one of the fathers of plant ecology. Warming was the first plant ecologist to ask questions about the composition of plant communities and the associations of species that made up these communities. The dynamics of vegetation change was emphasized first by North American plant ecologists. In 1899 H. C. Cowles described plant succession on the sand dunes at the southern end of

Lake Michigan. The development of vegetation was analyzed by the American ecologist Frederick Clements (1916) in a classic book that began a long controversy about the nature of the community.

With the recognition of the broad problems of populations and communities, ecology was by 1900 on the road to becoming a science. Its roots lay in natural history, human demography, biometry (statistical approach), and applied problems of agriculture and medicine.

The development of ecology during the twentieth century followed the lines developed by naturalists during the nineteenth century. The struggle to understand how nature works has been carried on by a collection of colorful characters quite unlike the mythical stereotypes of scientists. From Alfred Lotka, who worked for the Metropolitan Life Insurance Company in New York while laying the groundwork of mathematical ecology (Kingsland 1995), to Charles Elton, the British ecologist who wrote the first animal ecology textbook in 1927 and founded the Bureau of Animal Population at Oxford (Crowcroft 1991), ecology has blossomed with an increasing understanding of our world and how we humans affect its ecological systems (McIntosh 1985).

Until the 1970s ecology was not considered by society to be an important science. The continuing increase of the human population and the associated destruction of natural environments with pesticides and pollutants awakened the public to the world of ecology. Much of this recent interest centers on the human environment and human ecology, and is called environmentalism. Unfortunately, the word *ecology* became identified in the public mind with the much narrower problems of the human environment, and came to mean everything and anything about the environment, especially human impact on the environment and its social ramifications. It is important to distinguish ecology from environmental studies.

Ecology is focused on the natural world of animals and plants, and includes humans as a very significant species by virtue of its impact. **Environmental studies** is the analysis of human impact on the environment of the Earth—physical, chemical, and biological. Environmental studies as a discipline is much broader than ecology because it deals with many natural sciences—including ecology, geology, and climatology—as well as with social sciences, such as sociology, economics, anthropology, political science, and philosophy. The science of ecology is not solely concerned with human impact on the environment but with the interrelations of all plants and animals. As such, ecology has much to contribute to some of the broad questions about humans and their environment that are an important scientific component of environmental studies.

Environmental studies have led to "environmentalism" and "deep ecology," social movements with an important agenda for political and social change intended to minimize human impact on the Earth. These social and political movements are indeed important and are supported by many ecologists, but they are not the science of ecology. Ecology should be to environmental science as physics is to engineering. Just as we humans are constrained by the laws of physics when we build airplanes and bridges, so also are we constrained by the principles of ecology when altering the environment.

Ecological research can shed light on what will happen when global temperatures increase as a result of increasing CO_2 emissions, but it will not tell us what we *ought* to do about these emissions, or whether increased global temperature is good or bad. Ecological scientists are not policy makers or moral authorities, and should not as scientists make ethical or political recommendations. However, on a personal level, most ecologists are concerned about the extinction of species and would like to prevent extinctions. Many ecologists work hard in the political arena to achieve the social goals of environmentalism.

Basic Problems and Approaches to Ecology

We can approach the study of ecology from three points of view: descriptive, functional, or evolutionary. The descriptive point of view is mainly natural history and describes the vegetation groups of the world—such as the temperate deciduous forests, tropical rain forests, grasslands, and tundra—and the animals and plants and their interactions within each of these ecosystems. The descriptive approach is the foundation of all of ecological science, and while much of the world has been reasonably described in terms of its vegetation and animal life, some areas are still poorly studied and poorly described. The functional point of view, on the other hand, is oriented more toward dynamics and relationships, and seeks to identify and analyze general problems common to most or all of the different ecosystems. Functional studies deal with populations and communities as they exist and can be measured now. Functional ecology studies **proximate causes**—the dynamic responses of populations and communities to immediate factors of the environment. Evolutionary ecology studies **ultimate causes**—the historical reasons why natural selection has favored the particular adaptations we now see. The evolutionary point of view considers organisms and relationships between organisms as historical products of evolution. Functional ecologists ask *how:* How does the system operate? Evolutionary ecologists ask *why:* Why does natural selection favor this particular ecological solution? Since evolution not only has occurred in the past but is also going on in the present, the evolutionary ecologist must work closely with the functional ecologist to understand ecological systems (Pianka 1994). Because the environment of an organism contains all the selective forces

ESSAY

Science and Values in Ecology

Science is thought by many people to be value free, but this is certainly not the case. Values are woven all through the tapestry of science. All applied science is done because of value judgments. Medical research is a good example of basic research applied to human health that virtually everyone supports. Weapons research is carried out because countries wish to be able to defend themselves against military aggression.

In ecology the strongest discussions about values have involved conservation biology. Should conservation biologists be objective scientists studying biodiversity, or should they be public advocates for preserving biodiversity? The preservation of biodiversity is a value that often conflicts with other values—for example, clear-cut logging that produces jobs and wood products. The pages of the journal *Conservation Biology* are peppered with this discussion about advocacy (see, for example, *Conservation Biology* February 2007 issue, Brussard and Tull 2007, Scott et al. 2007).

There will always be a healthy tension between scientific knowledge and public policy in environmental matters . . .

Scientists in fact have a dual role. First, they carry out objective science that both obtains data and tests hypotheses about ecological systems. They can also be advocates for particular policies that attempt to change society, such as the use of electric cars to reduce air pollution. But it is crucial to separate these two kinds of activities.

Science is a way of knowing, a method for determining the principles by which systems like ecological systems operate. The key scientific virtues are honesty and objectivity in the search for truth. Scientists assume that once we know these scientific principles we can devise effective policies to achieve social goals. All members of society collectively decide on what social goals we will pursue, and civic responsibility is part of the job of everyone, scientists included. There will always be a healthy tension between scientific knowledge and public policy in environmental matters because there are always several ways of reaching a particular policy goal. The debates over public policy in research funding and environmental matters will continue, so please join in.

that shape its evolution, ecology and evolution are two viewpoints of the same reality.

All three approaches to ecology have their strengths, but the important point is that we need all three to produce good science. The descriptive approach is absolutely fundamental because unless we have a good description of nature, we cannot construct good theories or good explanations. The descriptive approach provides us maps of geographical distributions and estimates of relative abundances of different species. With the functional approach, we need the detailed biological knowledge that natural history brings if we are to discover how ecological systems operate. The evolutionary approach needs good natural history and good functional ecology to speculate about past events and to suggest hypotheses that can be tested in the real world. No single approach can encompass all ecological questions. This chapter uses a mixture of all three approaches and emphasizes the general problems ecologists try to understand.

The basic problem of ecology is to determine the causes of the distribution and abundance of organisms. Every organism lives in a matrix of space and time. Consequently, the concepts of distribution and abundance are closely related, although at first glance they may seem quite distinct. What we observe for many species is that the numbers of individuals in an area vary in space, so if we make a contour map of a species' geographical distribution, we might get something similar to **Figure 4**.

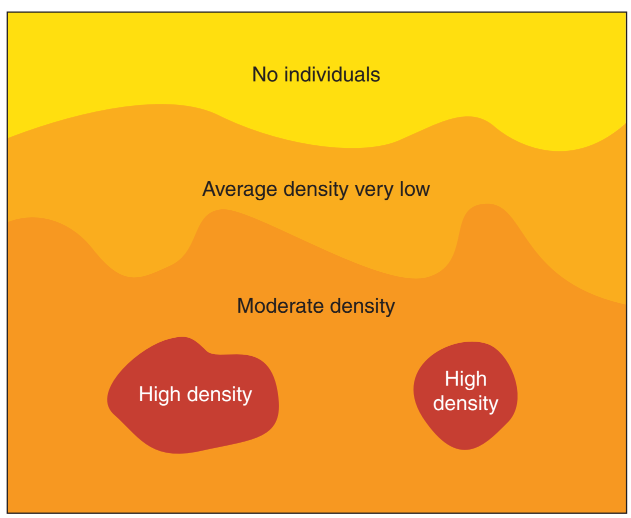

Figure 4 Schematic contour map of the abundance of a plant or animal species.

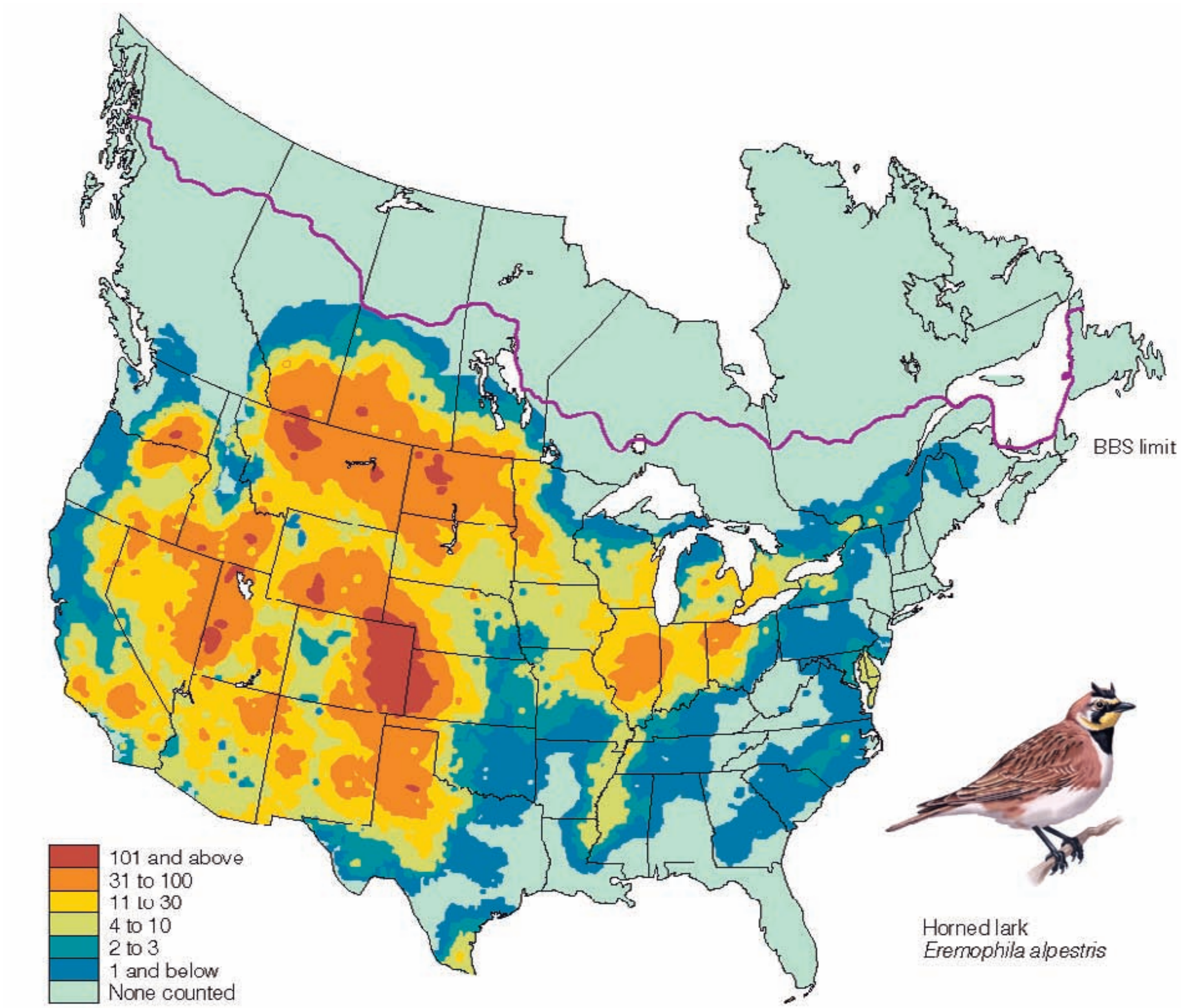

Figure 5 Abundance of the horned lark in North America from 1994 to 2003. Data are from the Breeding Bird Survey (BBS). Maximal abundance of this bird is reached in the short grass prairie of western Kansas and Nebraska and eastern Colorado. (From Sauer et al. 2005.)

Figure 5 illustrates this idea for the horned lark of North America. Horned larks are most common in the prairies of eastern Colorado and in western Kansas and Nebraska, and are absent altogether in Florida. Why should these patterns of abundance occur? Why does abundance decline as one approaches the edge of a species' geographic range? What limits the eastern and northern extension of the horned lark's range? These are examples of the fundamental questions an ecologist must ask of nature.

Similarly, the red kangaroo occurs throughout the arid zone of Australia (**Figure 6**). It is absent from the tropical areas of northern Australia and most common in western New South Wales and central Queensland. Why are there no red kangaroos in tropical Australia? Why is this species absent from Victoria in southern Australia and from Tasmania? We can view the average density of any species as a contour map, with the provision that the contour map may change with time. Throughout the area of distribution, the abundance of an organism must be greater than zero, and the limit of distribution equals the contour of zero abundance. Distribution may be considered a facet of abundance, and distribution and abundance may be said to be reverse sides of the same coin (Andrewartha and Birch 1954). The factors that affect the distribution of a species may also affect its abundance.

The problems of distribution and abundance can be analyzed at the level of the population of a single

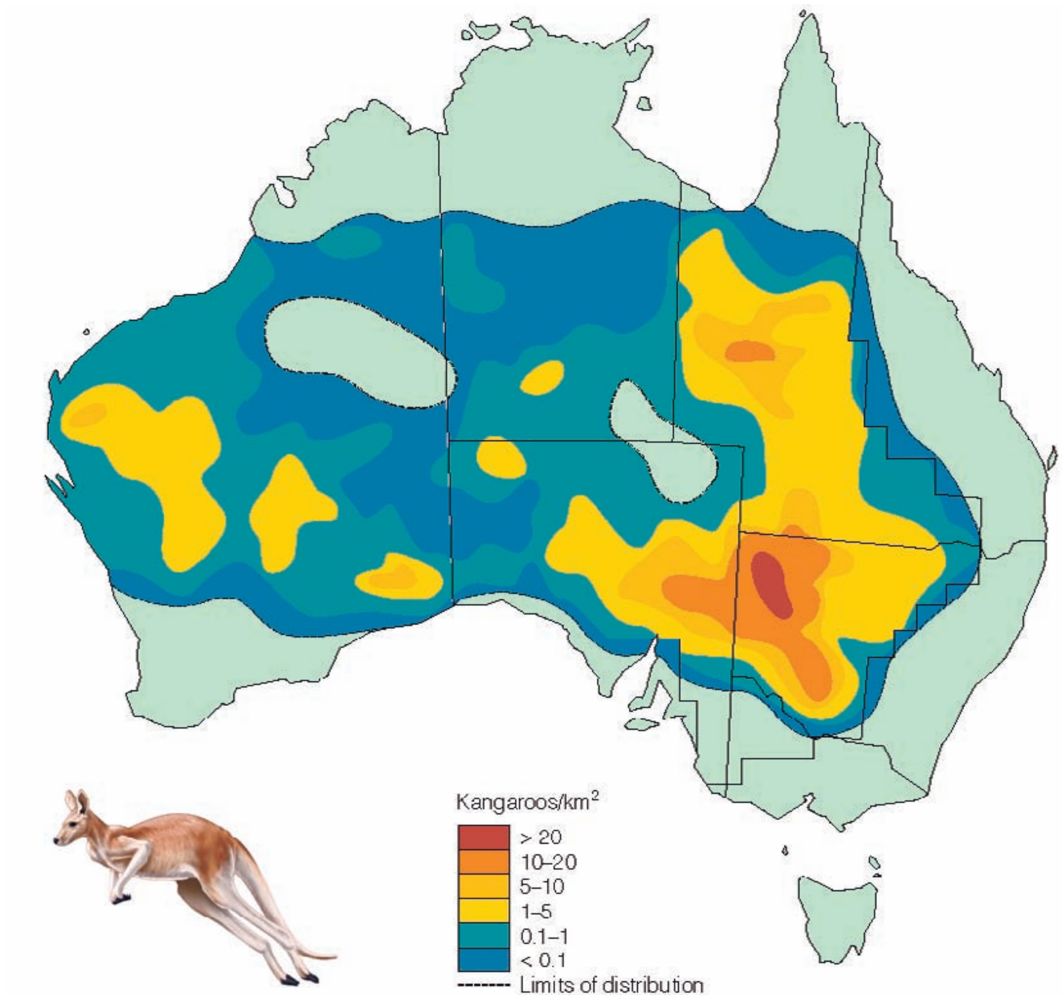

Figure 6 Distribution and abundance of the red kangaroo in Australia. Data from aerial surveys, 1980–1982. (From Caughley et al. 1987.)

species or at the level of a community, which contains many species. The complexity of the analysis may increase as more and more species are considered in a community; consequently, we will first consider the simpler problems involving single-species populations.

Considerable overlap exists between ecology and its related disciplines. Environmental physiology has developed a wealth of information that is needed to analyze problems of distribution and abundance. Population genetics and ecological genetics are two additional foci of interest that we touch on only peripherally. Behavioral ecology is another interdisciplinary area that has implications for the study of distribution and abundance. Evolutionary ecology is an important focus for problems of adaptation and studies of natural selection in populations. Each of these disciplines can become an area of study entirely on its own.

Levels of Integration

In ecology we are dealing primarily with the five starred (*) levels of integration, as shown in **Figure 7**. At one end of the spectrum, ecology overlaps with environmental physiology and behavioral studies of individual organisms, and at the other end, ecology merges into meteorology, geology, and geochemistry as we consider landscapes. Landscapes can be aggregated to include the whole-Earth ecosystem, which is called the **ecosphere** or the **biosphere**. The important message is that the boundaries of the sciences are not sharp but diffuse, and nature does not come in discrete packages.

Each level of integration involves a separate and distinct series of attributes and problems. For example, a population has a density (e.g., number of deer per square kilometer), a property that cannot be attributed